

YIELD, SEED PROTEIN PERCENTAGE, AND  
PHYSIOLOGICAL TRAITS IN SIMULATED AND FIELD CROPPING SYSTEMS

BY

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Dedicated to my wife Phyllis  
my sons Louis, Frederick,  
and my parents  
Louis Albert and Elizabeth--

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The extent to which physiological traits contribute to seed yield of soybeans (*Glycine max* L. Merrill) is poorly understood. Relationships among physiological traits and yield were studied in 15 field experiments. Materials were 12 random and selected F1 determinate genotypes from two crosses whose parents differed in seed protein percentage (SP%) [SPF]. Studies included yield and SPF associations, comparisons of physiological and visual estimation of seed filling duration (SPD), and their stability across environments.

A simulation model of soybean reproductive growth was developed to examine hypotheses about relationships among physiological traits and yield. The model incorporated a new concept, the rate of dry matter allocation to seed (DMAC) defined as the rate of linear harvest index (HI) increase. Hypotheses resulting from simulations were field tested for two years at Gainesville, Florida.

when the high protein parents were the highest yielding parents, correlations between yield and EPP were ambiguous or negative, as they usually are when high protein parents are the lower yielding parents.

Reproductive Period Duration (RPD), the ratio of final harvest index (HI) to RPD, started simultaneously with Effective Filling Period (EFP), but ended three to seven days later. Correlations between RPD and EFP ranged from  $r=0.30$  to  $0.89^{**}$ . Stage 55 was reached 10 to 16 days before linear seed growth started. The period 55-57 did not adequately estimate either EFP or RPD.

Simulations predicted positive associations of yield with RPD ( $R^2=0.18^{**}$ ) and seed growth rate (SGR) on a land area basis ( $R^2=0.81^{**}$ ), and negative associations of CRAC with yield ( $R^2=0.18^{**}$ ) and SGR ( $R^2=0.85^{**}$ ).

Field results were similar in sign and magnitude to simulation results. Yield was positively associated with RPD ( $R^2=0.06$  vs  $0.18$ ), 55-57 ( $R^2=0.08$  vs  $0.12^{**}$ ), SGR ( $R^2=0.61^{**}$  vs  $0.81^{**}$ ), and individual seed growth rate ( $R^2=0.06$  vs  $0.18$ ), and negatively associated with CRAC ( $R^2=0.03$  vs  $0.18$ ). Weak associations with yield and highly significant genotype by environment interactions diminish the usefulness of RPD as a selection criterion. Negative correlations ( $-0.05$  to  $-0.31$ ) between CRAC and EFP suggest a self-destructive mechanism, but its nature remains undetermined due to inconsistent and nonsignificant correlations of EFP with CRAC and EFD estimates.



## CHAPTER I INTRODUCTION

IN ORDER TO INCREASE soybean yielding and har-  
vestable yield through breeding, it would be helpful to  
understand the complex interactions of plant  
characteristics and processes that ultimately lead to  
yield. The identification of physiological traits that are  
closely associated with yield may allow their use in  
breeding programs. Some of these factors are seed protein  
percentage, length of the seed filling period, seed growth  
rate on an individual seed and on a land area basis, rate of dry  
matter allocation or partitioning of dry matter into seeds,  
amount of vegetative biomass present at the beginning of  
seed growth, and potential maximum rate of biomass  
production of the crop.

Of these factors, usually seed protein percentage has  
been negatively associated with yield (Johnson and  
Johnson, 1970; Tate and Morris, 1964; Orth et al., 1970a,  
1971b and Morris, 1970), with some exceptions (Orth et al.,  
1970a; Shannon et al., 1972).

Despite the usual negative correlations between seed  
yield and seed protein percentage, lines which combine high  
seed yield with high seed protein percentage have been  
produced (Thorne and Fehr, 1970; Bartels and Kinosh, 1972;  
Simpson and Milroy, 1969).

If the negative association between yield and seed protein percentage was primarily the result of tight linkages or pleiotropic effects, or both, the chance of achieving high yield and high seed protein percentage would be small. However, the negative associations usually found between these two traits may tend to be positive, if the high protein parent was also the high yielding parent, if linkages were reversed in the high protein parent, and if pleiotropic effects were negligible.

The application of yield component analysis, that is, individual seed weight, seeds per pod, and seeds per unit of land area has not led to substantial yield increases due to component compensation (Beale and Adams, 1970). Therefore, other approaches are needed to determine how seed yield can be increased. Factors that produce significant and consistent yield increases must be identified before any application to practical breeding procedures is feasible.

In this work, I will examine how soybean yield is achieved at the organizational level of the processes that ultimately lead to yield. Analyses done at a lower organizational level probably would mask the predominant trends.

The model expression for seed yield is

$$\text{Seed yield} = \int_{t_1}^{t_2} (dW/dt) dt \quad (1)$$

The terms  $W$ ,  $w$  and  $t$  are the initial and final stages of seed dry matter accumulation,  $W$  is the mass of seeds growing per unit of land area, and  $t$  is the time.

However, it appears that equation (i) can be simplified. Dyll and Lappala (1978) observed that individual seed growth is constant during much of seed filling. Similarly, Harvey and Wilson (1971a) observed that seed dry weight accumulation on a land area basis is also linear. Therefore, by assuming  $dW/dt$  is constant, equation (i) becomes

$$\text{Seed yield} = WOE + EPP \quad (2)$$

where  $WOE$  is the rate of seed dry weight accumulation per unit of land area, and  $EPP$  is Effective Filling Period defined by Conway et al. (1973) as the ratio of mean seed weight to its rate of growth during the linear phase.

Equation (2) shows that at the highest organizational level,  $WOE$  is the process that integrates all other plant processes leading to yield, and that the length of the period which this process takes place is a critical yield limiting factor.

Positive associations between yield and the length of seed filling have been reported (Harvey and Wilson, 1971a; Dyll and Lappala, 1978; Day et al., 1980; Moore, 1981). In some cases, the strength of this association was rather low (Conway et al., 1973; Baskin, Baskin and Wilson, 1982). Moore (1981) reported that yields exhibited a plateau at

### Seed filling periods

Similarly, earhead yield has not shown consistent highly significant positive correlations with RGR. Bawden (1978) observed a highly significant positive correlation between yield and RGR, while Manning and Wilson (1974), Bell and Leggett (1974), and Taylor and Bellar (1974) observed that the dependence of yield on RGR was rather small. At the individual seed level, Bell (1978) and Bell and Leggett (1978) also observed disappointingly low associations between yield and the rate of individual seed growth (RGR<sub>ind</sub>).

It should be noticed that genotypes in the studies cited above usually were unrelated, highly selected, reduced variation. In order to adequately represent trends within populations used by breeders, the associations of yield with the length of seed filling, RGR, and RGR<sub>ind</sub> should be determined using representative samples of random genotypes within populations.

Part of the difficulty in studying the association between RFR, RGR, and yield is due to the cumbersome methods available for the determination of RFR and RGR. The many replications needed to obtain precise RGR estimates due to the large CV's of dry weight traits reported by Carter et al. (1971) render this method impractical. Visual estimates of the length of seed filling become easy to obtain after Fehr and Caviness (1977) defined precise phenologic stages for soybeans. However, the correspondence

of visual estimates with physiologically defined estimates of seed filling duration has not been reported.

The influence of additional plant processes and characteristics on EPP, RGR, and ultimately yield, needs to be determined. Recently, Salade Benito et al. (1994) defined Dry Matter Allocation Coefficients (DMAC), as the ratio of linear harvest index (HI) increases. This new concept that accounts for the loss of assimilates partitioned from vegetative organs to seeds, in dry weight terms, showed strong and weak negative associations, respectively, with the length of seed filling and yield.

The timing of HI increases during most of seed filling allows for the characterization of a new and potentially useful physiological estimate of the length of seed filling. This concept is called Reproductive Period Duration (RPD), and is defined as the ratio of final HI to DMAC, when both of these traits are calculated disregarding foliage losses. Therefore, RPD is an estimate of the period of linear HI increases, much like EPP is an estimate of the period of linear seed growth.

The approach followed in this work was to develop a simulation model of soybean reproductive growth which allows the examination of the effects of each of the main factors that influence yield. Such a model would also allow examination of the influence of each factor on yield and other physiological traits independently of other factors. A representative sample of simulated genotypes was

generated through sensitivity analysis of the model and used to develop hypotheses on the dependence of yield on RFR, NFR, PFR, the amount of initial biomass (IBWAI) present at the beginning of seed growth, the potential maximum net biomass production (PBWAI) of the crop, and GDDC. The simulations under these factors were also studied. The hypotheses developed using simulated genotypes were then field tested for two years using two populations of detached genotypes.

This approach has the advantages of combining work on theoretical physiology with field work. The implications to physiology and breeding of the model predictions were validated through extensive field work. This approach has seldom been undertaken successfully, because it requires the availability of a suitable simulation model designed specifically for such purposes.

Objectives of this work were:

- (1) To determine the nature and strength of the association of yield with seed protein percentage within and across environments in two soybean populations whose high protein parents were also the high yielding parents;
- (2) To determine the correspondence between physiological (RFR and NFR and visual GDDC) estimates of the length of seed filling, and their stability across environments in detached genotypes;

- (ii) To determine the strength of the positive association of yield with EFP, EFP, and EFP-EF within and across environments using simulated as well as selected and random field-grown genotypes.
- (iii) To determine the association of yield with them in field-grown soybeans, and the association of yield with GGR in simulated and field-grown soybeans.
- (iv) To determine the relationships among GGR, estimates of the length of seed filling, yield, and seed protein percentage.

Chapters in this Dissertation generally progress from the consideration of the association of yield with seed protein percentage to the associations of yield with factors such as the length of seed filling, GGR, and GGR-EFP. Chapter II deals with yield-protein relationships from a breeder's perspective. The potential for using high yielding parents as the high protein parents to obtain positive rather than negative relationship between these traits is examined. Yield-protein relationships across environments are also examined to determine if correlations become more negative in lower yielding environments.

In Chapter III comparisons are made between EFP, EFP, and EFP-EF to determine if these three estimates could be used interchangeably. If they can be used interchangeably, the earlier deconvolution of EFP-EF with respect to the other two estimates would make the use of EFP-EF preferable. A new, precise method is described to determine EFP and EFP from only

three seedlings is presented. Comparisons of the seedling across environments and the broad sense heritabilities of these estimates of the length of seed filling are also examined to determine which of these traits would be the better selection criterion.

In Chapters IV through VI, the influence of DPHD, PHD, and SHC on the relationships of yield with SPV and SH, as well as on the dependence of the length of seed filling on SHC, is examined using a simulation model of soybean reproductive growth.

A simulation model of soybean reproductive growth is presented in Chapter IV. The purpose of the model was to examine the relationships among physiological traits and yield. Chapter IV focuses on the relationship between yield and the length of seed filling (SPV, PHD, and SH-ST), to determine if one of these traits would be helpful as a selection indirectly for higher yield in breeding programs. Random genotypes from two populations were used in the comparisons of yield with SPV and SH-ST, because they are a more representative sample of the populations breeders use.

Chapter V deals with the association of yield with DPHD and SH. Previous determinations of DPHD on a whole plant basis were obtained by sampling twice (three weeks after R5 and near R7). Similarly, SH estimates precise enough to detect significant differences between genotypes with few replications were obtained using a more practical method than the currently available ones.



In Chapter VI, the associations of  $WAC$  with the length of seed filler and grain, and the existence of a self-destructive mechanism of some sort, suggested by the negative associations of  $WAC$  with mean test grains, are reported. The possibility that the higher  $W$  seed density of genotypes with higher seed podicle percentages would be the driving force for a self-destructive mechanism is also examined.

Finally, Chapter VII summarizes the main results of this work, and places the associations in a broader context. A new theoretical approach to breeding higher yielding systems using physiological limits is outlined, along with a practical approach. The experimental work needed to test the feasibility of the proposed practical approach is also discussed.

CHAPTER II  
ASSOCIATIONS BETWEEN YIELD AND SEED PROTEIN CONCENTRATION  
WITHIN AND AMONG ENVIRONMENTS

INTRODUCTION

Dryland soils are an important protein source. Studies have shown that seed yield and seed protein percentage are negatively correlated traits (Johansen and Schimken, 1956; Ross and Ferris, 1964; Ryck et al., 1970; Bartels and Hinson, 1971; Ellis and Burton, 1971), with some exceptions (Ryck et al., 1970; Shannon et al., 1972). These studies showing negative correlations have been performed using genotypes derived from crosses in which the high protein parent was a lower yielding line, with few exceptions (Ross and Burton, 1971; Shannon et al., 1972).

The high protein percentage of some exotic genotypes may be simply a manifestation of their good adaptation. If that were the case, efforts to obtain high protein adapted genotypes from exotic x adapted crosses would be futile according to Thorne and Fehr, (1970). However, Bartels and Hinson (1971) presented evidence which suggested that high protein stress per se did not significantly influence yield. They concluded that lower yields resulted from factors other than high protein genes contributed by the low-yielding, high-protein parents.

If the negative association between yield and seed protein percentage was primarily the result of tight linkage or pleiotropic effects, or both, the chances of combining high yield and high seed protein percentage would be very small. But if the high protein parent was also the high yielding parent, the negative associations usually found between these two traits may tend to be positive, if linkage was removed and otherwise little or no pleiotropic effect.

Despite significant negative correlations between seed yield and seed protein percentage, it is possible to identify lines which combine high seed yield with high seed protein percentage and good agronomic traits, when appropriate selection methods are applied (Thorne and Peck, 1970; Harwig and Hinson, 1972; Simpson and Wilson, 1974). Thorne and Peck (1970) reported that three-way crosses of inbred x adapted x adapted genotypes produced were superior lines for yield and protein percentage than two-way crosses of inbred x adapted genotypes. Similarly, Harwig and Hinson (1972) found that the chances for obtaining productive lines with high seed protein percentage were greatly enhanced if selections were made from lines, or even better, mixed background materials raised when from the same cross.

Hinson (unpublished) observed that environmental factors can have a strong influence in the negative association between yield and seed protein percentage.

high-yielding plots of the cultivars 'Johanna' and 'Baron' and lower seed protein percentage than low-yielding drought-stressed plots. However, Byth et al. (1988) reported correlations between yield and seed protein percentage that were inconsistent in magnitude and direction, among different soybean populations grown favorable and drought-stressed environments. Thus further work is needed to determine if correlations between yield and seed protein percentage become more negative in low-yielding environments.

A strong negative correlation between soybean seed protein and oil percentages has been reported by several authors (Johnson and Johnson, 1958; Byth et al., 1988a and 1988b; Spruiell et al., 1973; Karkali and Elmer, 1972; Shannon et al., 1973; Simpson and Wilson, 1981). This probably due to the negative correlations between yield and seed protein percentage, and between the latter and oil percentage. In this study to maximize the amount produced per unit of land area of either protein or oil, or both, is yet to be determined. Caldwell et al. (1984) showed that predicted gain from selection for total protein per unit area was maximized by increase of seed yield or seed yield plus protein percentage. The yield of protein did not change in three of four cases when the seed protein percentage was significantly increased by several cycles of recurrent selection (Hale and Burton, 1970). However, yield of oil decreased in three of four cases after several

cycles of recurrent selection for high seed protein percentage. Future selection experiments should further determine if the yield of proteins and oil is more strongly associated with soybean seed yield or with seed protein and oil percentages, respectively.

In this work, soybean genotypes from two crosses in which the high protein parent was also the higher yielding parent were used. Random genotypes were used in 12 of 14 experiments; in the other two experiments genotypes were selected to represent differences in yield and seed protein percentage.

Objectives were: (I) to determine if the association between yield and seed protein percentage tends to be positive, when the high protein parent in the cross is also the higher yielding parent. (II) to determine if the negative association between yield and seed protein percentage is more negative in low yielding environments, and (3) to determine the strength of the associations between yield of proteins and oil with seed yield, and seed protein and oil percentages, respectively.

#### Materials and Methods

The materials used in these experiments were 40 randomly Group VII and VIII, 87 soybean genotypes from two crosses, 'Hemlock' x 'Horton' and Hemlock x 'Tree-101', and their parents. These materials were chosen to represent two soybean populations from the breeding program of Dr. Knott

Blaine at Gainesville, Florida. Bessie is the parent common to both strains. It is an old, low-yielding standard seed protein (40%) variety. Sutton is a moderately high-yielding Kentucky Group VII variety with approximately 41% seed protein. The other parent, P48-478, is an advanced genotype similar to Sutton in maturity, that produces moderately high yields with approximately 40% seed protein.

Cultures were random in 14 of 14 field experiments. In all cases the respective parents served as checks. In 1960, 1961, and 1962 experiments the parents were replicated four times, while the derived lines were replicated twice, resulting in a total of 48 entries per experiment. In 1963, genotypes from both strains selected to represent differences in seed yield and seed protein content, were combined in each experiment and replicated three times.

The test designation and location of 14 experiments included in this work are presented in Table I.1. The following convention was used to designate these tests: First the year expressed with two digits, followed by the initial letter of the location, the test number, and in the case of 1960, 1961, and 1962, by either the letter 'W' for the genotypes from Bessie x Sutton, or 'P' for the genotypes from Bessie x P48-478. In test 60-0-1-P, 'Mountain' a released high yielding variety of Kentucky Group VII, was included as an additional check. In 1963,

Table 1.1: Test Designation, year, location, and parameter of genotype in 14 field experiments.

Test	Year	Location	Parents
80-Q-1-B	1980	Gainesville, FL	Bonnie x Nylon
80-Q-3-B	1980	Gainesville, FL	Bonnie x P66-618
80-Q-3-B	1980	Quincy, FL	Bonnie x Nylon
80-Q-3-B	1980	Quincy, FL	Bonnie x P66-618
80-Q-3-B	1981	Gainesville, FL	Bonnie x Nylon
80-Q-3-B	1981	Gainesville, FL	Bonnie x P66-618
80-Q-3-B	1981	Quincy, FL	Bonnie x Nylon
80-Q-3-B	1981	Quincy, FL	Bonnie x P66-618
80-A-1-B	1982	C. Aron Farm, FL	Bonnie x Nylon
80-A-1-B	1982	C. Aron Farm, FL	Bonnie x P66-618
80-Q-1-B	1982	Gainesville, FL	Bonnie x Nylon
80-Q-1-B	1982	Gainesville, FL	Bonnie x P66-618
80-Q-1	1983	Gainesville, FL	Both Crosses
80-Q-2	1983	Gainesville, FL	Both Crosses

Tests SI-D-1 and SI-D-2 had 18 and 20 entries, respectively.

In 1980, 1981, and 1982 a total of six yield tests, two per season, were performed at the University of Florida Appling Farm, in Gainesville, Florida (29° 30' N latitude). The soil was an Alameda fine sand (a heavy siliceous hyporthumus *Gomphonema* Paleudalf), with a pH of approximately 5.2. The two 1981 tests were conducted at the same location in Gainesville, Florida. In 1980 and 1981 a total of four yield tests, two per season were conducted at the North Florida Research and Education Center, Quincy, Florida. The other two yield tests were performed at the University of Florida Green Acres Farm, near Gainesville, Florida.

Climatological data for the 1981 and 1982 growing seasons taken at the nearby Appling Farm Weather Station are summarized in Tables 2.2 and 2.3. Test SI-D-2 was the only one in which sprinkler irrigation was used as needed during the season. In all other cases, the plants relied on rainfall as their only source of water.

In all cases, randomized, complete blocks were used. Plots consisted of four rows 5.8 m apart, and 3.1 m long, except for Test SI-D-2 where 3.4 m long rows were used.

Tests SI-D-1-B and SI-D-2-F were established on 3 and 21 June, respectively, while Tests SI-D-1 and SI-D-2 were established on 18 and 22 June, respectively. Florida was



Table 1-2. Climatological data for Gainesville, Florida: 1 June through 1 November, 1983.

Date	Average Daily Temperature		Daily Totals		
	Max.	Min.	Windspeed	Precip.	Transp.
6/20-6/27	33.1	26.6	16.8	43.3	348.4
6/28-6/34	33.3	27.4	12.3	48.6	351.5
6/13-6/20	33.3	26.7	16.4	36.7	305.4
6/21-6/28	34.4	26.9	18.5	37.8	300.8
6/29-7/6	33.8	28.1	1.3	43.3	304.3
7/6-7/13	33.8	30.1	38.7	37.8	364.1
7/13-7/20	33.7	30.8	44.3	34.1	359.8
7/20-7/27	33.8	30.8	48.7	37.3	364.4
7/27-8/3	33.8	30.4	28.1	37.4	368.6
8/3-8/10	32.8	32.3	34.3	34.5	343.8
8/10-8/17	33.4	34.8	1.7	32.4	330.3
8/17-8/24	34.4	31.3	184.8	34.4	334.3
8/24-8/31	33.8	33.3	0.3	31.4	378.3
8/31-9/7	33.4	34.8	17.4	34.4	400.2
9/7-9/13	33.3	31.3	74.1	30.4	364.8
9/14-9/21	33.7	31.1	24.4	38.3	379.8
9/21-9/27	34.4	32.7	44.3	27.3	330.1
9/28-10/5	34.4	34.3	3.4	28.8	348.8
10/6-10/13	31.3	26.4	17.4	21.8	303.4
10/13-10/20	27.7	28.3	8.4	24.3	181.1
10/20-10/27	28.8	23.3	17.4	17.3	194.3
10/27-11/3	24.3	23.3	8.3	18.8	184.3

(1) transpiration: 100% below 100% relative humidity.

Table 2.2 Climatological data for Gainesville, Florida;  
1 June through 1 November, 1981.

Dates	Average Daily Temperature		Monthly Totals		
	Max.	Min.	Rainfall	Pos. Days	PRN(1)
	°F		in		mm
6/10- 6/17	32.8	20.7	66.5	34.1	169.1
6/18- 6/24	32.5	19.2	66.5	36.7	169.8
6/25- 6/31	32.8	21.8	1.5	41.8	169.8
6/10- 6/31	32.8	21.8	134.5	75.7	570.4
6/25- 7/1	32.6	21.5	49.2	35.8	273.8
7/2- 7/12	32.4	21.1	21.8	32.2	269.8
7/13- 7/23	32.2	22.5	14.3	40.2	129.2
7/24- 7/31	32.2	22.2	17.1	31.4	272.8
7/27- 8/2	32.4	22.4	24.8	38.1(2)	242.8
8/3- 8/9	32.6	22.2	21.1	29.4	145.2
8/10- 8/16	32.8	22.4	3.2	24.4	129.2
8/17- 8/23	32.5	22.5	6.4	32.2	273.8
8/24- 8/30	32.4	22.4	8.2	34.4	287.8
8/31- 9/6	32.8	22	12.2	37.1	217.2
9/7- 9/13	32.7	22	12.7	35	274.2
9/14- 9/20	32.5	22	14.2	34.2	272.2
9/21- 9/27	27.2	22	12.2	34.4	218.8
9/28-10/4	27.7	22	8.2	32.4	245.2
10/5-10/11	28.8	21.8	7.2	28.4	171.2
10/12-10/18	27.4	22.2	14.2	32.2	129.2
10/19-10/25	27.6	22.2	18.2	22.2	145.2
10/26-11/1	28.7	11.8	8.2	34.7	157.2

(1) Monthly Average Daily Maximum Temperature.

(2) Not available.

previously tilled and fertilized with phosphorus and potassium according to the recommended practice for the area.

Between previous sowings in these fields exhibited good nodulation, an *Bradyrhizobium japonicum* inoculation was used. In all cases good nodulation was confirmed near the flowering stage. Seeds were planted 5 to 6 cm deep in rows with a broadcast-sowed cover seed at the rate of 10 seeds per meter of row. Weeds were controlled by a broadcast pre-emergence application of 1.3 kg/ha s.i. of alachlor, and by machine cultivation and hand weeding during the growing season. Soil insects were preventively controlled with a pre-emergence broadcast application of 1.3 kg/ha s.i. of chlorpyrifos. In both years insect pests were controlled during the growing season with applications of 0.5 kg/ha s.i. of azinphos.

Harvest seeds were harvested with a self-propelled plot combine from 1.0m from each of two central rows per plot that had been previously trimmed at each end. Seeds were placed in labeled cloth bags and dried for three hours at approximately 50 °C in a forced air oven, then placed under same conditions for a week until seed moisture content was approximately 10%, then weighed. Seed yields were expressed as kg/ha.

Data from seed genotypes in the 1982 and 1983 years at Quincy were deleted due to poor plant stands. In 1982, seeds from both replications of each genotype in each

experiments were halved for protein and oil determinations. In all other cases seed protein and oil percentages were obtained from individual plots. In all cases, seed protein and oil percentages were determined from 40 g samples, at the USDA Southern Regional Research Center in Peoria, Illinois, following their standard procedures.

Additional analyses of the data were performed using Statistical Analysis System (SAS) version 79.3 (SAS/Inst and Council ed., 1979). Differences for yield, seed protein, and oil percentages among genotypes within experiments were tested by the analysis of variance procedure (ANOVA), and compared using Duncan's multiple range test at the 5 % significance level. The analyses of variance of yield and seed protein percentage for each cross, combined across 1982 and 1983, were performed using the ANOVA procedure according to the model presented in Table 2.4. Environment (E) and genotype (G) were assumed to be random. Variance components were estimated using the expected mean squares presented in Table 2.4 where

$\sigma^2_D = (D-1)/D$  = genetic component,

$\sigma^2_{DG} = (D-1)(G-1)/D$  = component due to genotype x environment interactions, and

$\sigma^2_e = D/G$  = component due to error

Broad sense heritability for yield and seed protein percentages were estimated according to the method proposed by Falconer (1960) as

Table 2.4 Expected value equations for the standard complete (linear) coded and over estimations

Source of variation	df	Mean	Expected mean squares	
			Expected mean squares (MS)	Random error (MS)
Between treatments	$t-1$	0	$\sigma^2_{\epsilon} + \tau\sigma^2_{\alpha} + \sigma^2_{\beta}(1) + \sigma\tau\sigma^2_{\beta}$	$\sigma^2_{\epsilon} + \tau\sigma^2_{\alpha}(1) + \sigma\tau\sigma^2_{\beta}$
Block (treatment)	$t(t-1)$	0	$\sigma^2_{\epsilon} + \tau\sigma^2_{\alpha} + \sigma^2_{\beta}(1)$	$\sigma^2_{\epsilon} + \tau\sigma^2_{\alpha}(1)$
Residual error	$q-1$	0	$\sigma^2_{\epsilon} + \tau\sigma^2_{\alpha} + \sigma^2_{\beta}(1) + \sigma^2_{\gamma}$	$\sigma^2_{\epsilon} + \tau\sigma^2_{\alpha}(1) + \sigma^2_{\gamma}$
Total in block	$t(t-1) + (t-1)$	0	$\sigma^2_{\epsilon} + \tau\sigma^2_{\alpha} + \sigma^2_{\beta}$	$\sigma^2_{\epsilon} + \tau\sigma^2_{\alpha}$
Error	$t(t-1) + (t-1) + 1$	0	$\sigma^2_{\epsilon}$	$\sigma^2_{\epsilon}$

$$S_{\text{env}}^2/\sigma^2_{\text{g}} = (r^2_{\text{g}} - r^2_{\text{g}})/1 + 1/r^2_{\text{g}}/r^2_{\text{g}}$$

The F tables proposed by McIntosh (1981) were used to test the different effects for randomized complete blocks combined over experiments. To test the effect of environments when both environments and genotypes were nested random, the following degrees of freedom were used:

- df is the numerator, df for environments,
- df is the denominator, df for blocks within environments or for genotype x environment (whichever was smaller).

### Results and discussion

#### PERFORMANCE OF LIGHT AND HEAVY DRAIN FERTILIZATIONS FOR YIELD AND SEED PROTEIN CONCENTRATIONS

In all cases, highly significant differences in seed yield and seed protein percentage were observed among random genotypes from each cross within experiments. The only exceptions were seed protein and oil percentages in 1980, where differences were not tested because seed samples were bulked for the laboratory determinations. Differences in yield and seed protein percentage were also highly significant when selected genotypes from both crosses were combined in two tests (3-5-1 and 3-5-2). The mean and standard deviation of yield and seed protein percentage for each experiment and cross are presented in Table 1.1.

Table 1-3. Mean and standard deviation of yield and seed protein percentages and their correlations among soybean genotypes in SALTATER experiments.

Soybean	Yield		Protein		Yield vs Protein
	Mean	Std. Dev.	Mean	Std. Dev.	
	kg/ha		%		r
80-0-1-0	1873	273	44.2	1.0	+0.434*
80-0-3-0*	1825	283	44.1	1.0	0.00
80-0-1-0	1820	438	44.4	0.7	+0.33
80-0-3-0*	1817	344	45.1	1.1	0.18
81-0-1-0	1854	295	43.8	1.1	+0.531**
81-0-3-0*	1708	382	43.3	1.3	+0.37*
81-0-1-0	1838	277	43.7	0.8	0.11
82-0-3-0*	1848	218	43.8	1.3	+0.33
82-0-3-0	1817	318	43.8	1.1	0.00
82-0-3-0*	1813	328	43.7	1.7	0.24
82-0-3-0	1808	344	43.7	1.0	+0.31
82-0-3-0*	1770	348	43.8	1.3	+0.05
83-0-1	2040	255	43.9	0.8	+0.34
83-0-2	2088	278	43.1	0.7	0.00

\*,\*\* Significant at 0.05,01 and 0.01, respectively.

Highly significant heritages by environment effects were observed for yield and seed protein percentage among certain genotypes from each cross in the overall analysis of variance combined over experiments (Table 3-4).

In both crosses, seed protein percentage had considerably higher broad sense heritability than yield. The values were 37.1 and 34.8 % for yield and 74.8 and 83.3 % for seed protein percentage, respectively among genotypes from *Roanoke x Bette* and *Roanoke x Phi-88*. Therefore fewer replications within and across environments are necessary to select for soybean seed protein percentage than for yield.

In general, these results are in agreement with the results of other authors (Burr and Farris, 1944; Byth et al., 1969, and Shannon et al., 1971), who found that heritability estimates were usually higher for seed protein percentage than for yield.

#### Relationships between Yield and Seed Protein Percentage

Eleven correlations between yield and seed protein percentage were nonsignificant. These negative correlations were significant or highly significant (Table 3-4). Similar phenotypic correlation values between yield and seed protein percentage were reported by several authors among soybean genotypes where high protein germplasm was also the lower yielding parent (Johnson and Hollman, 1958; Burr and Farris, 1944; Byth et al., 1969; Martens and Kinney,



Table 1.6. Mean squares from the analysis of variance combined over experiments for yield and seed protein percentage among random genotypes from two crosses.

Source	df	Yield	df	Seed Protein Percentage
----- Randoms x Reps -----				
Environments	3	2,178,883**	3	26.12**
Reps (Env.)	8	175,879*	8	.23
Genotypes	74	313,353*	74	8.23**
Gen. x Env.	178	127,848**	178	.79**
Error	204	47,814	204	.44
Mean		1814		42.31
C.V.		14.4		3.4
----- Randoms x Reps-Env -----				
Environments	3	888,842*	3	7.84
Reps (Env.)	8	285,313**	8	4.23**
Genotypes	74	171,023*	74	11.72**
Gen. x Env.	178	189,128**	178	6.86**
Error	221	85,034	221	0.57
Mean		1487		41.72
C.V.		14.4		3.8

\*, \*\* Significant at 5% and 1% level, respectively.

1971). In these two populations correlations between yield and seed protein percentage were similar to previously reported results in sign and magnitude. If linkages are important in negative relationships between protein and yield, correlation phase linkages evidently persisted in Sardin and P20-100.

The size and magnitude of the correlations between yield and seed protein percentage showed considerable variation across environments, within crosses (Table 3-3). The  $r$  values were between 4.11 and  $-0.10^{**}$  among the genotypes from Bourke x Sutton, and between 5.11 and  $-0.27^{**}$  among the genotypes from Bourke x P20-100. In environments as variable as these, experiments should be replicated across several environments to determine the average association between yield and seed protein content.

Mean yields ranged from low to moderate (Table 3-3). The lack of very low or high yielding environments prevented determining if seed protein percentage tends to increase in lower yielding environments.

#### Relationships between Seed Protein and Oil Percentages

Negative correlations between seed protein and oil percentages were significant and in most cases highly significant (Table 3-7). The magnitude of the negative correlations were above  $r=-0.30$ , except for Sarda 10-0-1-0 and 10-0-1-0. In general, these results are in agreement with results of many authors (Johnson and Robinson, 1955;

Table 2.7. Phenotypic correlation coefficients between seed protein and oil percentages in various soybean lines.

Experimental line(s)	Protein vs Oil	Experimental line(s)	Protein vs Oil
	*** p ***		*** p ***
80-0-1-8	-0.34*	80-0-1-7	-0.53**
80-0-1-9	-0.33*	80-0-1-8	-0.62**
81-0-1-8	-0.67**	81-0-1-9	-0.78**
81-0-1-9	-0.82**	81-0-1-8	-0.82**
82-0-1-8	-0.78**	82-0-1-7	-0.81**
82-0-1-9	-0.86**	82-0-1-8	-0.82**
82-0-1 (n=10)	-0.87**	82-0-2 (n=20)	-0.47*

\*,\*\* significant at 5% and 1%, respectively.

Spill et al., 1949a and 1949b; Shannon et al., 1972; Huxson and Wilson, 1981).

#### Yield of Protein and Oil and Their Association with Seed Yield and Seed Protein and Oil Percentages

In all cases, the variation in the amount of protein and oil produced per unit of land area was almost entirely explained by the variation in seed yield (Table 2.8). Two of 18 correlations between yield of protein on an area basis and seed protein percentage were significant (Table 2.8). Six of 18 correlations between yield of oil on an area basis and seed oil percentage were significant, three at the 5%, level. Thus in general, seed yield should be increased to increase the amount of protein produced per unit area, while the amount of oil produced per unit area could be increased by either yield or seed oil percentage increases.

#### Conclusions

Correlations between seed protein percentage and seed yield were nonsignificant or negative in several environments among random and selected genotypes from two crosses, in which the high-protein parents were also the high-yielding parents. Correlations similar in sign and magnitude usually have been reported when the high protein parents of the crosses are the lower yielding parents. Therefore, weak negative associations can be expected

Table 2.6. Phenotypic correlation coefficients between yield of protein and oil, seed yield, and seed protein and oil percentages, respectively in various experiments.

Treat	n	yield of	yield of	yield of	yield of
		Protein	Protein	Oil	Oil
		vs Seed Yield	vs Protein PERCENT.	vs Seed Yield	vs Oil PERCENT.
Experiment 1					
80-0-3-0	37	0.93**	-0.18	0.93**	0.31*
80-0-3-7	43	0.93**	0.09	0.93**	0.13
80-0-3-0	37	0.93**	-0.30	0.93**	0.17
80-0-3-7	43	0.93**	-0.89	0.93**	0.23
80-0-3-0	37	0.93**	-0.30	0.93**	0.49**
80-0-3-7	43	0.93**	-0.64	0.93**	0.37**
80-0-3-0	37	0.93**	0.25*	0.93**	0.89
80-0-3-7	43	0.93**	-0.13	0.93**	0.93**
80-0-0-0	37	0.93**	0.30	0.93**	-0.87
80-0-3-7	43	0.93**	0.30*	0.93**	0.30*
80-0-0-0	37	0.93**	0.30	0.93**	0.09
80-0-3-7	43	0.93**	0.30	0.93**	0.30*
80-0-0	38	0.93**	-0.80	0.93**	0.84
80-0-3	39	0.93**	0.37	0.93**	-0.28

\*,\*\* Significant at 5% and 1% level, respectively.

between yield and seed protein percentage if either higher or lower yielding parents are used as the high protein source. If linkages are important in negative relationships between protein and yield, repulsion phase linkages evidently prevailed in Nelson and Pilchik.

The sign and strength of the correlations between yield and seed protein percentage can show considerable variation across environments, while crossover correlations ranged from  $r=0.51$  to  $-0.51^*$  in one cross and from  $r=0.51$  to  $-0.17^*$  in another cross, over six environments. Therefore to estimate the average yield-protein relationship studies should be performed across several environments.

Associations between yield and seed protein percentage across low and medium-yielding environments did not show a tendency to become consistently negative and stronger when yields were lower. The lack of high-yielding environments prevented adequate testing of the hypothesis that seed protein percentage tends to decline in low-yielding environments.

In nearly all cases, yield of protein and oil were almost exclusively a function of seed yield, and usually were not associated with seed protein and oil percentages, respectively. However, in six of 14 cases positive correlations between yield of oil and seed oil percentage were significant or highly significant, but the  $r$  values were always considerably lower than those between yield of

oil and seed yield. These results suggest that seed yield should be increased to increase the amount of protein produced per unit of land area, while either seed yield or seed oil percentage can be increased to increase the production of oil per unit area.

CHAPTER 121  
COMPARISONS AMONG EFFECTIVE FILLING PERIOD, REPRODUCTION  
PERIOD DURATION, AND SE-ET IN SEEDING POTENTIAL

Introduction

Positive correlations between yield and different estimates of the length of seed filling have been reported (Barney and Weber, 1971a; Ehl and Leggett, 1972; Gough et al., 1973). However, the successful use of the length of seed filling to indirectly select for yield among breeding lines has not been found in the literature. Thus, selection for yield itself appears to be the method currently used by breeders. The lack of methods for a precise, physiologically sound, and easily obtained estimate of the length of seed filling in many genotypes prevents its widespread use. Little evidence exists concerning the correspondence between visual and physiologically defined estimates of seed filling duration. Finally, information on the repeatability of estimates of seed filling duration across environments would be useful.

A physiological estimate of the length of seed filling, effective filling period (EFP), was defined by Gough et al. (1973) as the ratio of mature seed weight to seed growth rate, has been used to a limited extent in soybean research. The method to estimate EFP as



individual pod basis for whole plants is cumbersome. On the other hand, estimation of EFP on a land area basis may lack precision, as may be inferred from the report of Carter et al. (1984). Several replications are needed to detect differences in dry weights caused due to the relatively high EFP's usually found in soybean seed growth analysis.

A simpler method to allow a precise estimation of EFP on a whole plant basis may depend on the use of the EFP concept in soybean research. Average individual seed growth rate (1984) on a whole plant basis showed a linear trend and low EFP's in several *Glycine max* soybean genotypes (Hanson 1972, unpublished). In this case plants were sampled at weekly intervals. The average weight of individual seeds on a whole plant basis was obtained by dividing the weight of seeds from each plant by the number of seeds present. These data suggest that only an early and a late sampling during seed filling would accurately estimate EFP. Previous estimates of EFP may then be obtained from an additional sampling at maturity. We compared EFP values obtained by this method to those from sequential samplings and found that EFP values resulting from the two methods were not significantly different.

An alternative would be to use another physiological estimate of the length of seed filling. The essentially constant harvest index (HI) increases during most of the soybean seed filling period (Hanson 1972, Spurr et al., 1974) allows for a simple, and physiologically

seed characterization of the length of seed filling based on the period of linear  $R_L$  increase. The Dry Matter Allocation Coefficient (DMAC), the ratio of linear  $R_L$  increase to total dryweight of fallen leaves, showed lower CV's than seed growth rate (SGR) on a land area basis (Belady-Sanders et al. 1984). This characteristic may double also provide us a new estimate of the length of seed filling. This concept was called Reproductive Period Duration (RPD), and defined as the ratio of final  $R_L$  to DMAC. Therefore, RPD is an estimate of the period of linear  $R_L$  increase, much like SFR is an estimate of the period of linear seed growth.

Visual estimates of the length of seed filling can be determined from ontogenetic stages of soybeans defined by Fehr and Seneweber (1977). Stage II is when a pod with seeds 1 cm in size appears at one of the four uppermost nodes of the main stem with a fully developed leaf. Stage III, the beginning of maturity, corresponds to the appearance of a pod with mature seeds on the main stem. These visual stages are easily observed and are widely used in the literature. The use of visual estimates of the length of seed filling would be more advantageous in breeding programs, if they proved to be physiologically sound, or if they were tightly associated with physiological estimates of the length of seed filling.

For indeterminate soybeans, stage II is not an adequate indicator of the beginning of linear seed growth

(Hewitt and Vezinier, 1974c). The beginning of rapid seed growth at Chippewa 64 showed a sequential pattern from the lower to the upper portions of the panicle, that lasted for more than three weeks, and R5 occurred near the end of that period. The timing of R5 with respect to the beginning of linear seed growth on determinate soybeans has not been reported.

The end of seed growth as physiological maturity coincided with R7 in several genotypes in one study (Hewitt et al. 1981), but in another study (Hewitt and Gaudinette, 1981) R7 occurred just before physiological maturity, and was not consistent over years. These studies were conducted on indeterminate genotypes. The unknown stage R7 may have a different timing with respect to physiological maturity in determinate soybeans. Hewitt (1979) observed that R7 started several days after R5 on determinate genotypes.

The comparative stability of RFP and R1-R7 across environments would suggest which of these traits would be a better selection criterion if their positive associations with yield were strong and stable. Effective Filling Period (RFP) is influenced by pod size and number in genotype by environment associations which may impair its usefulness as a selection index in a breeding program Ogil and Leggett, 1971). If a new physiological estimate of the length of seed filling based on fixed R1 and R8/R5 were defined, perhaps it would be more stable than RFP across

environments, because HI is a relatively stable trait according to several authors (Hickey, 1949; Johnson and Major, 1970; Sprague et al., 1966). The broad sense heritability of these traits will indicate their repeatability across environments. Information such as this would help one decide which estimates of seed filling duration (if any) would be most useful in breeding higher yielding systems.

The objectives of this work were: (i) to compare HY with a new estimate of the length of seed filling based on the period of linear HI increase and with HI-HI; (ii) determine the extent to which estimates cover simultaneously; and (iii) determine if they can be used interchangeably to characterize seed filling duration of determinate systems on a whole plant basis. Additional objectives were to determine the comparative stability of these three traits across environments and their broad sense heritabilities relative to yield. This information would be useful to indicate which of these traits would be a better selection criterion, if further studies show that they are closely associated with yield.

### Materials and methods

Factual details from five field experiments are reported in this chapter. The materials and methods for Tests HI-D-1 and HI-D-D-F in 1982, and Tests HI-D-1 and HI-D-2 in 1981, were described in Chapter 14. Then in this

section. additional procedures dealing with visual documentation of R1 and R7 and crop growth analysis are described. Also a fifth experiment, Test 43-6-3, which was designed to collect data on R1-R7 is described. Only Test 43-6-1 was sporadically analyzed during the growing season.

For the purposes of this work, Test 43-6-1 was designed to collect data on seed yield and the vegetative stages R1 and R7. Crop growth analysis was performed on the other experiments (except Test 43-6-3), along with a determination of mature seed yield on a whole plot basis as described in Chapter II.

In both years average reproductive stages R1 and R7 of plants in each plot were visually determined three times per week using the methods of Fehr and Cassman (1977). Each plot was sampled twice for crop growth analysis. The first sampling was taken three weeks after each genotype reached R1, and the last sampling was taken just before R7. In 1942, additional intermediate samples were collected at weekly intervals on six genotypes from each cross and their respective parents. Samples were also collected among the repeatedly sampled genotypes. Samples consisted of above-ground portions of three random plants taken from border rows of each plot. Each plant was placed in a labelled paper bag, dried in a fanned-air draft oven at approximately 70 °C for at least 48 hours, then weighed. Seeds were separated from other plant materials and weighed.

Average SI of each plot was calculated as the ratio of seed weight to plant weight, disregarding fallen leaves, at the time of each sampling. In 1982, the increasing of SI increase during seed falling was tested for each sequentially sampled genotype. Dry Matter Allocation Coefficient (DMAC) was estimated for all genotypes in both years, using data from early and late sampling dates: three weeks after R5 and just before R7. An additional estimate of DMAC was obtained for the 17 genotypes from both crosses that were sequentially sampled in 1983, using the procedure described by Salas-Barrera et al. (1984).

Harvest Index of mature plants was determined by the procedure previously described. Reproductive Period Duration (RPD) of genotypes in each plot was calculated as the ratio of SI at maturity to DMAC.

Individual seed growth rate (ISGR) on a whole plant basis was obtained from the genotypes that were sequentially sampled in Tanta SI-2-1-8 and SI-2-2-9, and from all the genotypes in Teta SI-2-1. In 1983, two procedures were used to estimate ISGR. In the first method, the average individual seed weight from three plants in each sampling date and plot combination was divided by their initial seed number, then averaged data as the average individual seed weight from the sequential samplings were fitted to a linear regression model to obtain ISGR. In the second method ISGR was estimated in a similar way, except that only data from the first and last

germinating ability were used. This latter procedure was also used to estimate time of germination in Tests 11-0-1. Average mature weight of individual seeds was determined for each plot from 100 seeds. Effective Filling Period was estimated for the genotypes that were separately sown in Tests 11-0-1-8 and 11-0-1-9, and for all the genotypes in Test 11-0-2, by dividing average individual weight of mature seeds by 1000.

The beginning of linear seed growth (BLSG) was calculated as the day in which predicted linear seed growth intercepted the x axis. The beginning of linear RI increase (BLRI) was calculated in a similar way, as the day in which predicted linear RI increase intercepted the x axis.

The end of linear seed growth (ELSG) was calculated as the day in which predicted seed growth reached mean mature seed weight. Similarly, end of linear RI increase (ELRI) was calculated as the day in which predicted RI increase reached the mean final RI value.

In 1913, Tests 11-0-1 had 16 random determinate genotypes from each cross between a Burton and Lincoln x P18-818 including the respective parents that were described in Chapter 10. The genotypes in Tests 11-0-1 and 11-0-2 were sown in Test 11-0-3.

Randomized complete blocks with two replications were used in Test 11-0-3. Plots were only one row, 2.5 m long and 2.5 m apart. The field experiment was established on 18 June 1913 in a field adjacent to Test 11-0-1 at the

University of Florida Agronomy Farm in Gainesville, Florida, 29 30° S latitude. The soil characteristics, general experimental procedure, data collection, and analysis were similar to those previously described in Chapter II for the other experiments.

### Results and Discussion

#### Linear Growth Index Increases During Seed Filling

In 1982, LI increased linearly with time ( $r^2=0.97$ ) during seed filling in all 17 genotypes tested by sequential analysis. The only exception was Brevard, where LI increases showed a slightly lower fit to the linear model ( $r^2=0.84$ ). Brevard, a released variety of different ancestry isolated as an additional check, also showed a linear LI increase ( $r^2=0.97$ ) during most of the seed filling period. A linear LI increase for genotypes of different parental backgrounds has been reported (Salido-Puentes, 1982; Specht and Sinclair, 1983b). Therefore the 1982 results obtained in genotypes from two sources support the idea that linear LI increases during most of seed filling is a commonest feature of determinate systems. Consequently, the concept of WAI may have widespread application for determinate systems, because it is based on linear LI increase, and would estimate the rate of dry matter allocation into seeds.



### Reproduction Period: Biomass Estimated From Three Samplings Only

The highly linear increase of SE during most of seed filling allowed the estimation of DMAC from only an early (three weeks after SI) and a late (near ST) sampling. In 1982 estimates of DMAC for 17 genotypes, based on two sampling dates and on sequential sampling throughout seed filling were positively correlated ( $r=0.71^{***}$ ) and statistically similar as measured by a paired  $t$  test. Consequently it was concluded that satisfactory estimates of DMAC could be calculated using data from an early and a late sampling during seed filling.

These results allowed a precise estimation of SEB from three sampling dates (three weeks after SI, near ST, and at harvest maturity) using few plants. Estimates of SEB obtained in this way exhibited relatively low CV's (between 0.040 and 0.070) among the genotypes from both years in 1980 years.

### Estimation of Effective Filling Period From Three Samplings Only

Average individual seed weights on a whole plant basis showed linear growth ( $R^2=0.91$ ) during most of seed filling for all 17 genotypes that were sequentially sampled in 1980 (S-0-1-8 and S-0-2-8). This linear seed growth allowed the estimation of SEB in two ways: using data from all the sequential samplings and using data from samplings

were three weeks after R3 and near R7- in 1982, estimates of LGR based on both sequential samplings and only two sampling dates, for a total of 12 phenotypes from both crosses were positively associated ( $r^2=0.77$ ) and statistically similar as revealed by a paired  $t$  test. Consequently, it was concluded that satisfactory estimates of LGR on a whole plant basis could be calculated using data from only one early and one late sampling.

These results allowed a precise estimation of RFR through reduced sampling of a few plants, similar to the methodology used to estimate RPD. Estimates of RFR obtained in this way had relatively low variability. The CV's ranged from 4.8% to 8.1% for the phenotypes from both crosses in two years.

#### Correlations among Average RGR and RFR estimated on a whole plant basis, and R3 in a variable number of phenotypes from the two crosses showed a consistent trend across genotypes and experiments (Table 2.1). In all cases, average RGR and RFR increased almost simultaneously. Values were always within the 95% confidence intervals. Furthermore, a strong positive association between RGR and RFR was found among genotypes within experiments (Table 2.2). Therefore, RGR and RFR were physiological events that occurred simultaneously in these dicotyledonous systems.

mean, and 74 percent of the respondents indicated that they would not change their frequency and use of food products. Additionally, respondents from the general US population

Trial	1977-1978-79		1979-80-81		1981-82-83	
	(n=4)	(n=4)	(n=4)	(n=4)	(n=4)	(n=4)
0.002	0.0 ± 0.0	-	0.0 ± 1.0	-	0.0 ± 0.0	0.0 ± 0.0
0.002	0.0 ± 0.0	0.0 ± 1.0	0.0 ± 1.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
0.05	0.0 ± 0.0	0.0 ± 1.0	0.0 ± 1.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
0.002	0.0 ± 0.0	-	0.0 ± 0.0	-	0.0 ± 0.0	0.0 ± 0.0
0.001	0.0 ± 0.0	0.0 ± 1.0	0.0 ± 1.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 1.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0

2005-2010, leading to more good results. With funding from the National Endowment for Human and Social Development, University of Illinois at Chicago.

Table 3.4 Phenotypic correlation coefficients for early 2000-mm, selection at fertilization and end of seed growth of intermediate genotypes from two strains, in two years.

Genotype	1997		1998		1999		2000	
	vs B200	vs B201	vs B1	vs B2	vs B1	vs B2	vs B1	vs B2
<hr/>								
Alameda 8 (B200) (n=8)	0.3000	0.3400	0.2000	0.2000	0.2700	0.14	0.14	0.44
Alameda 8 (B201) (n=8)	-	-	0.3000	-	-	-	-	0.2000
Alameda 8 (B1-B2) (n=8)	0.3400	0.3000	0.2000	0.2000	0.43	0.3000	0.30	0.30
Alameda 8 (B1-B2) (n=8)	-	-	0.3000	-	-	-	-	0.2000
<hr/>								
<hr/>								
Belle Geyser Combined 1 (B200 n=18)	0.3000	0.3000	0.3000	0.3000	0.3000	0.3000	0.3000	0.3000

1. The Alameda 8 (B200) were in 1997-98 and 0.30 1999, and positively also beginning later seed growth, mid-terminating Alameda 8 (B200) and Alameda 8 (B201) were in 1997-98, mid-terminating Alameda 8 (B200) and Alameda 8 (B201) were in 1997-98.

On all cases, the stage R5 preceded both R1R2 and R1R1 by 10 to 14 days (Table 1.1). Therefore, on the average, R5 was not an accurate estimate of either R1R2 or R1R1 as a whole plant basis. However, R5 showed consistently high positive correlations (0.90-0.91) with R1R2 and also with R1R1 among genotypes, across populations and years (Table 1.2). Therefore, R5 was a precise relative, although not accurate, indicator of both R1R2 and R1R1 on determinate systems.

The occurrence of R5 several days prior to R1R2, on determinate genotypes, contrasts markedly with the timing of these two events in indeterminate plants. In the latter, R5 occurred near the end of a sequential period of about three weeks during which events at different plant levels initiated and growth ceased and resumed, (Table 1.1). Thus, an accurate visual indicator of the physiological initiation of rapid seed growth for arboresc plants remains to be determined.

#### Correlations Stage R5 of Linear Seed Growth, End of Linear Growth, and R1

In each experiment, the genotypes reached R1R2 an average of three to six days before R1R1 (Table 1-1). These differences were significant, except among the genotypes from Bataan a factor is that R1-R1-R1. The rapid loss of leaves that usually occurs towards maturity probably resulted in an extended period of R1 increase.

In all cases, positive correlations were found between  $GLD$  and  $SLD$  across genotypes, within experiments (Table 3.1). But the correlations were not consistently significant across experiments. This lack of consistency may be due to differences in the genetic background of the genotype tested, or to environmental factors, because in 1982 the genotypes in the two populations were planted in different field experiments (plots 12-4-3-E and 12-4-3-F).

In two out of three experiments, average  $GLD$  on a whole plant basis, and  $ST$ , were reached almost simultaneously. Their 95 confidence intervals overlapped (Table 3.1). The genotypes  $Line$   $Mancha$  x  $Burton$  in 1982 were exceptions. They reached  $SLD$  on average of five days later (Feb. 24) than  $ST$  and their 95 confidence intervals did not overlap. This was the only case in which  $GLD$  showed a weak positive association with  $ST$  across genotypes. In the other two experiments, the positive association was significant or highly significant (Table 3.1). Contrary to the findings of Tabery et al. (1981), these inconsistent results and associations suggest that  $ST$  is not always an accurate visual indicator of physiological maturity in soybean plants. This inconsistency may be expected, because the stage  $ST$  is not consistent among genotypes across years according to Hoopel and Crampton (1981). And because  $GLD$  may be inconsistent among genotypes across years.

Plants reached ELBI seven to 11 days after they reached ET (Table 3.1). Pairwise associations between these two stages were not consistently significant across experiments (Table 3.1). Thus ELBI occurred near ET, and the time between ET and ELBI was not consistent across genotypes and environments.

#### Comparisons across Effective Tillers Perged, Reproductive Phase Duration, and RPD

In two of the three experiments ETP of genotypes from both sources averaged about a week shorter (P=0.45) than RPD (Table 3.2). In the other experiment, the average lengths of ETP and RPD were not significantly different, probably due to the lack of differences observed between ELBI and ELBI (Table 3.1). Significant differences for ETP within tests were found only among the genotypes in Test 13-6-1-6. In all cases, RPD and RPD-ET exhibited highly significant differences among genotypes within environments, except for RPD which not in Test 13-6-1-6.

Associations between ETP and RPD were positive within experiments (Table 3.1), but varied across experiments. Longer RPD's and inconsistent associations between ETP and RPD were probably due to differences between ELBI and ELBI, because ELBI and ELBI occurred simultaneously in different replications. In all cases, ETP and RPD began simultaneously but RPD finished at different times after ETP.

TABLE 2. 1 Means and 95 confidence intervals for effective nesting effort (days), reproductive period (incubation period), and 50-50 of parents from two groups, in two years.

Year	1996		1997		Total	
	10-01	10-02	00-03	10-03	10-02	10-03
Reproductive Period (days)						
10-01	28.1 $\pm$ 2.6	-	33.2 $\pm$ 3.1	-	29.4 $\pm$ 3.0	-
10-02	41.0 $\pm$ 1.1	40.2 $\pm$ 1.3	41.4 $\pm$ 2.0	32.4 $\pm$ 1.4	42.0 $\pm$ 1.1	-
10-03	42.2 $\pm$ 0.4	44.3 $\pm$ 0.8	42.8 $\pm$ 0.8	41.3 $\pm$ 0.8	43.0 $\pm$ 1.2	-



Table 3.4 Phenotypic correlation coefficients ( $r$ ) among  
Extremum Filing Period (EFP), Reproductive  
Period Duration (RPD), and RS-RT.

	EFP vs RPD	EFP vs RS-RT	RPD vs RS-RT
	<b>(198)</b>		
Removal to Britain ( $n=3$ )	0.81**	-0.33	0.73*
Removal to Britain ( $n=49$ )	"	"	0.48**
Removal to FWS-RTS ( $n=3$ )	0.33	0.75*	0.14
Removal to FWS-RTS ( $n=43$ )	"	"	0.17**
	<b>(199)</b>		
Both Classes Combined = Parents ( $n=20$ )	0.62**	0.66**	0.43

\*,\*\* Denotes significance at 0.05 and 0.01 levels,  
respectively.

Visual estimates of the length of seed filling (S5-S7) averaged eight to 12 days longer (P40.00) than RFP (Table 3.4). The period S5-S7 was also significantly longer than RPO, except for genotypes from Bascoba x F40-616 (p=0.05). Therefore, S5-S7 was not an adequate indicator of either RFP or RPO, primarily because determinate plants reached S5 several days before they reached R400 or R401, and the timing of R400, R401 and S7 were usually different.

Correlations of S5-S7 with both RFP and RPO within experiments were always positive, but the magnitude of associations were not consistent across experiments. Therefore, the visual estimate of the length of seed filling S5-S7 was not a consistent accurate or precise indicator of either RFP or RPO within environments.

#### Comparative Stability of Effective Filling Period, Anthesis to Filling Duration, and S5-S7 Across Environments

The three estimates of the length of seed filling, RFP, RPO, and S5-S7, exhibited highly significant genotype by environment interactions except the six genotypes from Bascoba x Botton that were studied across 1960 and 1961 (Table 3.4). Therefore, in terms of stability across environments, it appears that neither RPO nor S5-S7 showed any advantage over RFP. Eyal and Leggett (1971) reported that RFP was least affected across environments, and for that reason they questioned its significance as a selection criterion.

Table 3.3. Total Squares from the analysis of variance combined across 1982 and 1983, for effective filling period (EFP), reproduction period (RPR), and R-E of four selected CV genotypes and their parents (Anjou and Hudson).

Source of Variation	df	EFP	RPR	R-E*
Environments	1	51.48	109.49	18.94
Blocks (Env.)	3	13.48	24.81	3.95
Genotypes	3	19.43	43.81	18.38
Gen. x Env.	3	14.87**	97.27**	28.83**
Error	66	5.48	11.34	1.79
CV		0.244	0.843	0.037

\* = Sum of Squares at 145.751.

Similar results were obtained when the stabilities of SI-RT and RPD were compared among larger numbers of genotypes. Within populations (Table 3.6), highly significant genotype by environment interactions were detected for SI-RT in both crosses, and for RPD in one cross.

To further test if the visual estimate of the length of seed filling (SI-RT) of genotypes from two crosses interacts with environments, different comparisons across experiments were done. In all cases, highly significant genotype by environment interaction effects for SI-RT were detected (Table 3.7). Variability within experiments for SI-RT was relatively low as the CV values show:

Based on the Heritability of Relative Filling Period,  
HYPOTHESIS 2: Yield Enlarges, Not SI-RT

The estimates of broad sense heritability for RPD was 16.7%, and for RPD and SI-RT were 0 among six genotypes from *Monarda* x *Helianthus*. Additional estimates of broad sense heritability for RPD were 0 among 11 genotypes from *Monarda* x *Helianthus* and 71.8% among 18 genotypes from *Monarda* x *Pinus*-*Pinus*. Additional estimates of broad sense heritability for SI-RT were also inconsistent across trials and crosses (Table 3.8). In the case of *Monarda* x *Helianthus*, the broad sense heritabilities for SI-RT and yield were similar, but they were inconsistent on the other crosses. These results suggest that the use of either physiological RPD and RPD

Table 3-4 Mean ingesta from the analyses of sections collected during 1983 and 1984 for reproductive female bivalves (BFB) and 21-87, of selected 27 genotypes from the present.

Genotype	Bivalvia 1983/84			Bivalvia 1984/87		
	df	Mean	SE-87	df	Mean	SE-87
Reproductive	1	188.83	55.33	1	207.43	213.33
Bivalvia (BFB)	3	31.04	2.83	3	8.48	3.88
Genotypes	26	66.13	43.13	0	68.88	16.55
BFB, n Gen.	16	66.4388	18.8888	0	13.33	8.2888
Genes	26	13.88	1.55	21	18.45	8.34
CV		8.686	0.036		8.887	4.343

CV = Coefficient of variation.



Table 3.4 Broad sense heritability of seed yield and plant  
density phenotypes from two crosses across  
different experiments.

Experiment	n	Yield	SD-SD
Experiment 1			
02-0-0-0 vs 01-0-0-1	8	34.7	18.8
02-0-0-0 vs 01-0-0-2	12	43.8	48.3
02-0-0-0 vs 01-0-0-3	16	"	41.8
02-0-0-0 vs 01-0-0-1	18	43.8	25.0
01-0-0-0 vs 01-0-0-2	18	43.3	58.4
01-0-0-0 vs 01-0-0-3	18	"	7.2

or visual estimates of the length of seed filling, as selection criteria should be practiced across environments in order to be effective.

### Significance

The linearity of SI increasing across several determinate soybean genotypes from two crosses was confirmed, consequently, the concept of DMAC, the rate of linear SI increase (estimated disappearing fallen leaves), may have widespread application for determinate soybeans. Such results allow for a potentially useful and physiologically sound characterization of the length of seed filling. Reproductive Period Duration (RPD), the ratio of final SI to DMAC, is an estimate of the length of the period of linear SI increase such like RPD is an estimate of the duration of linear seed growth.

Estimates of DMAC and RPD on a whole plant basis obtained from only one early and one late sampling date were equivalent to estimates obtained from sequential samplings performed throughout seed filling. Reproductive Period Duration and RPD with relatively low CV's were calculated. Dispersibility from DMAC and RPD obtained from three samplings.

In all cases, mean RSGD and RSLD occurred simultaneously in determinate genotypes from two crosses. Plants reached R1 10 to 14 days before either RSGD or RSLD. No associations among these three stages were positive and



strongly (PC2, 11%) although R2 was an inaccurate indicator of R2G2 and R2G1 on determinate genotypes. It was an absolutely precise relative measure.

Plants reached near R2G1 three to six days after near R2G2 on each genotype-environment combination. In two of three cases, differences were significant. Stage R2 coincided with R2G2 on two of three experiments.

Two physiological estimates of the length of seed growth (EPF and EPG) were positively associated but varied in degree of association. They started at the same time, but EPG finished up to one week after EPF.

The period R2-R7 was 4 to 13 days longer than EPF, and slightly longer than EPG. The visual estimate of the length of seed filling R2-R7, was not a consistent, precise, and accurate estimate of either EPF or EPG.

Estimates of broad sense heritabilities for EPF, EPG, and R2-R7 were inconsistent. They were similar, and sometimes lower, than for yield. Therefore, the use of EPF, EPG or R2-R7 as selection criteria in soybean breeding, appears to be somewhat limited. Also, selection for longer seed filling periods would have to be practiced across environments, if it is to be effective.

CHAPTER IX  
ASSOCIATIONS BETWEEN SEED AND FILLING PERIOD ESTIMATES  
FROM SIMULATED AND FIELD GROW SYSTEMS

Introduction

Barry and Weber (1974c) found that seed yield was more a function of the length of seed development than of the rate of seed growth on a land area basis, among eight soybean genotypes. Boli and Leggett (1971) found a positive association between Effective Filling Period (EFP) and seed yield of two genotypes. Based on similar results, Day et al. (1969) suggested that yield improvements in the future may be possible by lengthening the filling period. However, the use of estimates of the length of seed filling in breeding programs to indirectly select for higher yielding soybeans has not been reported.

Visual estimates of the length of seed filling are easily determined. Probably for that reason reports on their association with yield are often found in the literature, especially after Fehr and Senesko (1977) described specific developmental stages. The period R1-R5 showed consistent positive associations with soybean yields among numerous genotypes in different environments (Murphy et al., 1979). David (1974) found a highly significant positive association between R5-R7 and yield of eight

late-maturing genotypes. Bonte (1951) reported a positive association between 35-55 and yield of several early-planted genotypes from different maturity classes. However, in three out of four experiments, yields began to plateau at the longest filling periods. Various visual estimates of the length of seed filling exhibited low variability ( $CV=0.212$  to  $0.541$ ) and were positively associated (0.61-0.71) with yield among genotypes with different seed growth constant (Bonte, Stevens and Hanson, 1951).

In studies where positive associations between yield and different estimates of the length of seed filling were found, associations were not consistently strong. While Murphy et al. (1979) found that the period 55-65 was the most highly associated with yield among numerous genotypes, the correlation coefficients ranged from 0.13 to 0.54. Bonte, Stevens and Hanson (1951) found that only about 10 % of the yield differences were explained by differences in visual estimates of the length of seed filling.

In the studies cited, associations between yield and different estimates of the length of seed filling usually were determined on unrelated genotypes that had already been selected for high yield, i.e., released varieties. In order to adequately represent needs within populations used by breeders, associations between yield and the length of seed filling should be determined on representative samples of random genotypes within crosses.

Shenoy and others (1983) observed that correlations between  $r_{100}$  and  $RGR$  were negligible ( $r = 0.01$ ,  $n = 10$ ;  $r = 0.06$ ,  $n = 11$ ) and  $r = 0.16$ ,  $n = 10$  among three groups of random soybean genotypes. If these results were confirmed among random genotypes in other genetic backgrounds, indirect selection for plant size associated at the height of seed filling would be questionable in soybean breeding.

The strength of the association between field and the height of seed filling remains important, however, even though the existence of genotype by environment interactions presented in Chapter III limits their practical application. Ultimately, seed yield is a function of the rate of seed dry weight accumulation on a land area basis (BOS), and of the duration of this process.

Another approach to study the dynamic interrelations of factors on plant growth, including BOS and duration, is the use of simulation models specifically developed for certain purposes (Riker, 1980; Penning de Vries and van Laar, 1981). Several simulation models have been developed with different purposes for soybeans and other crops (Riker 1980). However, most of them are complex, or have been developed to study crop management strategies. A simple simulation model that incorporates the concept of the rate of dry matter allocation over seeds (BOS) and simulated the primary purpose of the model was to examine hypotheses that have implications in soybean breeding, rather than trying to make soybean growth. As

Important assumption of the model used here is that weather plays no role in growth limit soybean yields only to the extent that vegetative dry matter restricts the production and development of seed.

The use of a simulation model would allow the examination of the type and strength of the association between yield and the length of seed filling, and also would require additional physiological traits which may influence the nature and strength of this relationship.

A third approach was taken to examine the relationship between yield and seed filling duration in soybeans. First, a simulation model of soybean reproductive growth was developed, and a simulated set of soybean genotypes was generated through sensitivity analysis of the model. The set of simulated genotypes was assumed to be representative of a population of soybean genotypes. Hypotheses about the type and strength of the association between yield, RFR, and RFD were developed using the simulated genotypes. Second, resulting hypotheses were field tested using random genotypes from the genome in one year, and in another year, genotypes used were selected to represent differences in yield and seed filling period duration. Additional objectives were to determine the nature and strength of the association between yield and RFR-RFD within and across environments, using field-grown soybeans.

## Materials and Methods

### Model Development

This model was developed to examine the association among different traits and physiological processes and their relationship with yield, in order to study hypotheses that have potential implications in breeding higher yielding systems. The model was intended to simulate soybean reproductive growth under non-stressed environmental conditions, which were assumed uniform throughout the seed-filling period. Thus the rate of potential maximum net biomass available for crop production (PMBM), after respiration, was maintained constant throughout seed filling. We used PMBM's of 130, 200 and 270 g/dm<sup>2</sup> a day of biomass. The last two values corresponded to the average values reported by Eliasziw and de Wjz (1974).

The model simulates soybean crop growth from the beginning of linear N increase (estimated disappearing fallen leaves) until maturity. It was assumed that events prior to that period influence primarily the amount of vegetative biomass at the beginning of seed growth (IBBM), and thus the leaf area index (LAI) and amount of seed set. For that reason IBBM is used as a model input. Values for IBBM used in the simulations were between 2000 and 3500 kg of dry weight/ha, which correspond to values found by Senfeli (1970), and Salgado-Sarmiento (1982).

It was assumed that leaflets account for 10% of DMAD, the rest being petioles and stems. Leaf area index (LAI) was calculated as the ratio of leaflet dry weight to specific leaf weight. An average specific leaf weight of  $0.1 \text{ g dry weight}/\text{dm}^2$  of leaf area was used to obtain LAI throughout seed filling.

The energy conversion efficiencies derived by Fournier de Vries (1979) to produce carbohydrates, proteins (with nitrate as the nitrogen source), lipids, and lignin from glucose were used to transform biomass production into vegetative biomass and seeds. It was assumed that protein has 16% N, and the content of N in leaflets was set at 0.3% based on data from Young et al. (1979). Petioles and stems were assumed to have 2.8 and 2.4% N, respectively, based on data by Harvey and Weber (1931) of protein formed from nitrate or from symbiotic nitrogen fixation were not distributed, because the energy efficiencies from both sources are similar according to Hardy and Saville (1979). Seeds were assumed to have a constant composition throughout seed growth as reported by Gaike-Mancuso (1982). Seed composition was set to 40% proteins, 30% lipids, 25% carbohydrates, 4% lignin, and 1% ash, but these values could be changed to simulate the effects of seed composition on other traits and processes. Based on these conversion efficiencies and compositions, one unit of glucose yields either 0.455 units of vegetative dry weight or 0.878 units of seed dry weight. The correct value was

sized by Sinclair and de Wit (1988).

Another model input is the rate of net increase (estimated disappearing foliage leaves),  $\Delta NAL$ , as defined by Salido Navarro et al (1984), which is maintained constant throughout seed filling. The range in  $\Delta NAL$  used was between 0.011 and 0.008 day<sup>-1</sup> because similar values were reported by these authors on some genotypes under good growing conditions.

### Model Description

A simple model written in BASIC was developed to account for the dynamic balance of carbon and other nutrients during soybean seed growth, on an energy equivalent basis (Appendix II). Semi-implicit integration is performed to upgrade each state variable with a time interval of 0.1 day, and the model outputs the state of the system on a daily basis with the values of each variable expressed in kg/ha. The initial inputs to the model are  $TMAR$ ,  $PMAR$ , and  $DMAC$ . The values of the initial inputs used in the sensitivity analyses are presented in Table 4.1.

The first step in the flow diagram of the system (Fig. 4.1) is to calculate the daily rate of net biomass production of the crop ( $PROD$ ) which is available for tissue synthesis after respiration. In this case the exponential formula based on  $PMAR$  and  $LAI$  derived by Sinclair and de Wit (1988) was used to calculate  $ECAR$ . Biomass production is



Table 4.1 Input variables for sensitivity analysis of the simulation model of siphon reproduction growth.

Variable	Units	Values Tested
Initial Stock (I <sub>0</sub> )	kg/ha	1500, 1550, 1600
Potential maximum net biomass production (P <sub>max</sub> )	kg/ha x day	150, 160, 170
Dry Matter Allocation Coefficient (DMAC)	day <sup>-1</sup>	0.013, 0.013, 0.013, 0.014, 0.015

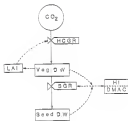


Figure 4.1 Flow diagram of the model of soybean reproductive growth.

transformed into vegetative biomass using energy equivalent values to form a vegetative dry matter pool.

Total seed growth rate (SGR) on a dry weight basis ( $\text{kg/ha a day}$ ) is estimated through successive iterations, as a function of the current plant dry weight and GDD. A predetermined maximum tolerance is set for a SGR value that allows GDD to remain constant, within a given iterational tolerance. The resulting pattern of seed dry weight accumulation follows a logistic curve with a long linear phase. An energy proportional to SGR on an energy equivalent basis is then subtracted from the vegetative dry weight pool. This feature allows the simulation of the effect of different compositions of vegetative organs as well as seed on other limits and processes by simply changing the energy equivalent ratios.

Any time SGR is smaller than RGR on an energy equivalent basis, the vegetative dry matter pool is increased accordingly. It was assumed that a negligible amount of leaf growth takes place during most of seed growth. Therefore, increases in the vegetative dry matter pool (if any) during seed filling, increase seed dry weight.

Since RGR is often greater than SGR on an energy equivalent basis in soybeans, there is a net loss of vegetative materials through translocation of assimilates to seeds. To account for the loss of assimilates from vegetative organs, the model destroys proportional

increments of leaf area, petioles, and roots as the basis of the energy equivalent value of green biomass instead of the 8 leaves used by the "self-destruct" model by Sinclair and de Wit (1976).

It was assumed that leaflet dry weight declines accounts for about 60% of the vegetative dry weight decline that occurs during seed filling. In terms of whole energy equivalent value, in this percentage figure are included the assimilate translocated to seeds, as well as the portion that is irreversibly lost as fallen leaves that were assumed to be 20% of the total dry weight decline. These assumptions are based on the higher nitrogen content of leaflets compared with petioles and roots (Sinclair and Weber, 1971 c), and seedling leaflet dry weight loss accounts for approximately half of the vegetative dry weight loss during seed filling (Sinclair and Weber, 1971 b).

Simulations are allowed to proceed until the available LAE is totally depleted; at that point it is assumed that maturity has been reached. The model then outputs the final status of the species. The duration of seed filling, calculated by the model, is reproductive period duration (RPD). Effective Filling Period can be calculated, then, as the ratio of final seed weight to the GR observed during the linear portion of seed growth.

A total of 45 simulated soybean genotypes was generated through sensitivity analysis of the simulation model of soybean reproductive growth, using the limited

inputs presented in Table 4.1. Data on the simulated genotypes were fitted to a linear regression model to examine the type and strength of the association among seed filling duration estimates, other physiological traits, and yield.

### Field Experiments

The hypotheses resulting from the simulations were field-tested using partial data from a total of 35 experiments. The materials and methods for all of them were described in Chapters II and III. Thus, in this section only additional procedures will be detailed.

YIELD data from two experiments performed at the Agricultural Research and Educational Center, Quincy, Florida, and Gainesville, Florida in 1980 and 1981, and at Green River Farm near Gainesville, Florida in 1980 were used. Additional data for yield and other traits detailed in Table 4.1, from five other experiments performed at Gainesville, Florida in 1980 and 1980 were also used. Irrigation was used to supplement rainfall in only one case (Treat 17-0-2).

Table 4.3. Variables measured in the experiment at Gainesville, Florida, in 1982 and 1983.

DATE	Number of Genotypes	VARIABLES
82-0-1-0	8	SP, SPO, SI-ST, Yield
82-0-1-0	48	SPO, SI-ST, Yield
82-0-2-0	8	SP, SPO, SI-ST, Yield
82-0-2-0	48	SPO, SI-ST, Yield
82-0-3	20	SI-ST, Yield
82-0-3	20	SP, SPO, SI-ST, Yield
82-0-3	80	SI-ST

## Results and Discussion

### Single Factor Analysis of Yield as a Function of the Model Inputs

To examine the dependence of yield on model inputs (IRRAE, PRAR, and DMAC), a single factor analysis was performed using simulated genotypes. By doing so, it is possible to determine the dependence of yield on one input at a time, while the others are held constant (Figs. 4-2.1, 4-2.2, and 4-2.3): at a constant IRRAE (1000 kg/ha), yield shows a nearly linear increase with PRAR increasing, and higher yields correspond to the lower DMAC values (Fig. 4-2.1a). Yield declines with increases in DMAC, and the highest yields correspond to the higher PRAR levels (Fig. 4-2.1b). Similarly, at a given PRAR (100 kg/ha a day), yield increases with IRRAE, and higher yields correspond to lower DMAC values (Fig. 4-2.2a), while yield declines with DMAC and higher yields correspond to higher IRRAE levels. Finally, at a given DMAC (0.015 day<sup>-1</sup>), yield increases with increases in either IRRAE or PRAR levels (Fig. 4-2.3a and 4-2.3b).

The above results will be useful in formulating strategies to increase soybean yield through breeding (Chapter VII).

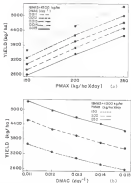


Figure 4.2-5: Seed yield as a function of Potential Seedling and biomass production (PMAC) at 400 kg/ha (a) and DMAC (day<sup>-1</sup>) at 0.001 day<sup>-1</sup> (b), at a constant initial biomass (10000), in simulated soybean genotypes.



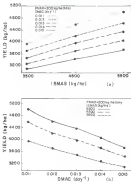


Figure 8.2.2 Seed yield as a function of biomass (Biomass) in (a), and Dry Matter Allocation Coefficients (DMAC) in (b), at a constant potential nitrogen net biomass production (7780), in simulated soybean production.

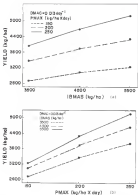


Figure 4.2-3: Seed yield as a function of initial biomass (IBMAE) in (a), and maximum seed biomass production (PMAX) in (b), at a constant DCP fixed allocation coefficient (DPAE), in simulated soybean genotypes.

### Associations Between Yield and Length of Seed Filling with RFP Genotype

A positive association between yield and RFP was predicted from 45 simulated soybean genotypes, and 17% of their yield variation was explained by the variation in RFP (Fig. 4.2). Field results showed that a large portion of the yield variation in different experiments was explained by the variation in RFP (Figs. 4.4, 4.5, and 4.6). In all cases, these associations were nonsignificant. The range in RFP among the genotypes in each RFP-RF was narrow (11 to 22 days), and genotypic differences for RFP were nonsignificant. Thus, it is not surprising that the association of yield with RFP (Fig. 4.4) was also nonsignificant.

A positive association between yield and RFP was predicted by the 45 simulated soybean genotypes, but the linear regression of yield as a function of RFP explained only 4% ( $R^2=0.48$ ) of the yield differences (Fig. 4.7). Results from two years of field experiments with 77 Delawarean genotypes from two crosses support the hypothesis formulated with the simulation model (Figs. 4.4, 4.5, and 4.6). In 1982 random genotypes were used to test this hypothesis, while in 1983, genotypes were selected to represent differences in yield and seed filling duration. In all cases, linear regression of yield as a function of RFP explained similarly a small portion of the yield differences.

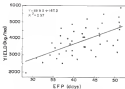


Figure 4.3. Seed yield as a function of Effective Flowering period (EFP), among simulated soybean genotypes

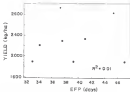


Figure 4-6: Seed yield as a function of Effective Filling Period (EFP), using selected PT soybean genotypes from Ransohr's Station as Test R2-0-1-0.

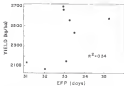


Figure 3.5— Seed yield as a function of Effective Filling Period (EFP), among selected F2 soybean genotypes from *Reynolds 7* P44-424 in Test 02-0-2-7.

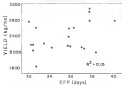


Figure 8.6. Seed yield as a function of Effective Filling period (EFP), among selected P1 soybean genotypes from crosses of Sakide and Rosendo x P44-437, in Test 81-3-2.

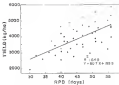


Figure 4 T. Seed yield as a function of Reproduction Period Duration (RPD), among simulated soybean genotypes.



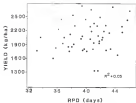


Figure 4.5. Seed yield as a function of Reproductive Period Duration (RPD), among random P7 soybean genotypes (from Roseoka station in Year 12-60) (a)

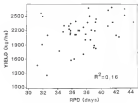


Figure 4.3. Seed yield as a function of Reproductive Period Duration (RPD), among random F2 soybean genotypes from Recombinant F16-618 in test 81-0-0-0.

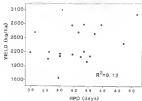


FIGURE 4.12 Yield yield as a function of reproductive period duration (RPD), among P3 soybean genotypes from Ranges 4 (R2000 and R4000) and Ranges 4 (R4000 and R4000), in Test 80-2-2

The relationship between yield and R5-R7 provided additional evidence for weak positive associations between yield and the length of seed filling period among random genotypes. In 1981, the linear regression of yield as a function of R5-R7 among random genotypes from two crosses produced a small portion of the yield differences (Fig. 4-11 and 4-12). The slopes of the predicted lines were not significantly different from zero. Similar results were observed in 1983, when the genotypes studied were selected to represent yield and seed filling differences. Although in these cases the associations between yield and R5-R7 were highly significant, only about 40% of the yield variation was explained by the linear regression model (Fig. 4-13 and 4-14). In all cases, genotypes with high and low yields were found when the periods R5-R7 were longer. Therefore, selection for long R5-R7 would not have necessarily implied selection for higher yields.

Since yield is a function of RGR and the duration of seed filling, these results indirectly suggest that RGR may be more important than the length of seed filling in determining the yielding ability of random genotypes.

#### FIGURE 4-11: Scatter Diagram of the Association Between Seed Yield and the Length of Seed Filling Periods (R5-R7) in 1981

In order to examine which factors influenced the weak positive associations between yield and different estimates of seed filling duration observed within experiments, the

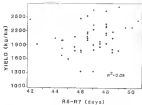


Figure 8.11. Seed yield as a function of the period H8-H7 among random P2 soybean genotypes from Noronka 8 during in Year 82-83-1-8.

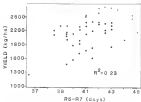


Figure 4.12 Seed yield as a function of the period RB-R7 using random 17 soybean genotypes from seasons 2000-2002 in Test 03-0-3-0

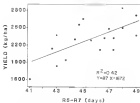


Figure 4.13. Seed yield as a function of the period RS-RT among P2 near-isogenic genotypes (see Materials & Methods and Materials APIS-455 as TEST PI-G-1).

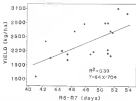


Figure 3.14. Seed yield as a function of the period R6-R7 among F7 soybean genotypes from Baccara X Sutton and Pioneer x P10-633 18 Test 13-9-3.



characteristics of simulated genotypes were included in a plot of yield versus EFP (Fig. 4-15). In this case only 18 simulated genotypes were used for demonstration purposes. The highest yield corresponded to the simulated genotype with lowest EFP, highest TMSA and PRAZ levels, and lowest DMAC.

The key weather simulation coefficients exhibited strong and weak negative influences, respectively, on the length of EFP and yield among simulated genotypes (Fig. 4-15). Field results showed close agreement with the simulations. In all cases, negative correlations were highly significant between DMAC and tillage period, emergence and senescence between DMAC and yield. A detailed analysis of field data on this subject is presented in Chapter VI.

Within a given DMAC level, increases in TMSA and PRAZ produced sharp yield increases, but EFP remained essentially constant among simulated genotypes (Fig. 4-15). Field results from two years support this hypothesis (Chapter VII). Therefore, the weak positive associations of yield with EFP and other estimates of the length of seed filling observed among simulated and field grown soybean genotypes within environments were probably caused by the differential influence of TMSA, PRAZ, and DMAC, on yield and EFP.

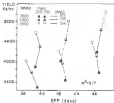


Figure 1-13. Factors influencing the association between seed yield and Effective Planting Period (EPP) among combined genotypes.

### Associations Between Yield and Length of Seed Falling Across Environments

The correlations between yield and EFP were nonsignificant and inconsistent across environments (years) among the genotypes from Kansas & Mexico (Table 4.3). Yield in 1982 was positively correlated with EFP estimated in 1982, but yield in 1983 was negatively correlated with EFP estimated in 1983. Thus, EFP was a poor predictor of yield across environments as it was within environments.

Similarly, the associations between yield and EPO were nonsignificant across years and crosses (Table 4.4). Therefore, EPO was a poor predictor of yield across as well within environments.

The lack of repeatability of EFP estimates across environments (years) was supported by the nonsignificant correlations between EFP estimates across 1982 and 1983 in both crosses (Table 4.5). Therefore, yield from each year was a better and more consistent predictor of yield across years than EFP, among the genotypes from both crosses.

The correlations between yield and E1-E2 across 1982 and 1983 were either nil, or positive and nonsignificant among the genotypes from both crosses (Table 4.6). The only exception was the nonsignificant negative correlation between E1-E2 estimated in 1982 and yield in Year E1-E2.

Estimates of E3-E4 showed low positive or no correlation across 1982 and 1983 among the genotypes from both crosses (Table 4.7). These results were probably due

Table 4.3. Phenotypic correlation coefficients (r) between seed yield and Effective Filling Period (EFP) across 1992 and 1993, among 216 selected P2 soybean genotypes from the Arica Research Station

Genotype	1992 Yield	1993 Yield	1993 EFP
1992 EFP	0.89	0.80	0.29
1992 Yield	-	0.91	-0.43
1993 Yield	-	-	0.15

Table 4-4: Phenotypic correlation coefficients ( $r$ ) between seed yield and Reproductive Period Duration (RPD) across 1993 and 1995, among selected PT soybean genotypes from the crosses.

TRAIT	1993 Yield	1995 Yield	1995 RPD
----- BONDURA x BARKER (m11) -----			
1993 RPD	0.65*	0.18	0.82
1993 Yield	-	0.32	-0.11
----- BONDURA x P41-422 (m12) -----			
1993 RPD	0.18	-0.87	0.18
1993 Yield	-	0.64*	-0.15

\* Significant at 500.0%.

Table A.1. Phenotypic correlation coefficients ( $r$ ) between yield and SD-ST scores (1982 and 1983 using PT system) genotypes from two crosses.

Traits	Yield		SD-ST		
	1982-83	83-84	83-84	83-85	84-85
===== BOLNISI X Haring =====					
1982 Yield	0.34 (ns)	0.33 (ns)	0.22 (ns)	0.17 (ns)	0.38 (ns)
1982 SD-ST	-0.23 (ns)	0.45 (ns)	0.28 (ns)	0.33 (ns)	0.34 (ns)
===== Bolnisi X P10-058 =====					
1982 Yield	0.34 (ns)	0.38* (ns)	0.42 (ns)	0.11 (ns)	0.24 (ns)
1982 SD-ST	0.31 (ns)	0.17 (ns)	0.33 (ns)	0.23 (ns)	0.25 (ns)

\* Significant at  $P=0.05$ .

is the highly significant (P<0.01) genotype by environment interactions for H1-H7 detected among the genotypes from both crosses and reported in Chapter III. Seed yields showed consistent positive associations across 1982 and 1983 within crosses (Table 4.5). Therefore, in general, yields in either 1982 or 1983 were better although not precise indicators of yield across years than H1-H7 among the genotypes from both crosses.

To test further if H1-H7 could be used as a selection criterion to predict the yield performance across environments among random genotypes, yield data from various experiments performed at Gainesville and Quincy, Florida in 1980 and 1981 were correlated with H1-H7 estimates in the same random genotypes at Gainesville, Florida, in 1982 and 1983. Again, the presence of inconsistent correlations between yield and H1-H7 across environments was observed (Table 4.6). Correlations were either low positive or negative, or nonexistent among the genotypes from both crosses. Similarly, correlations of average yields across six environment year combinations and H1-H7 measured in 1982 and 1983 were, respectively,  $r = -0.01$   $n=33$  and  $0.07$   $n=15$ , for the genotypes from *Monarch x Bahia*, and  $r = -0.23$   $n=18$  and  $0.11$   $n=11$  for the genotypes from *Monarch x P45-618*. These results suggest that the use of H1-H7 estimates obtained in any one year to predict yield of random genotypes across years is not feasible. It appears that estimates of the length of seed tillers would

Table 4.4. Phenotypic correlations among means (r) between plots established at Gainesville, Florida (n=194) and U.S. and yields of various P<sub>2</sub>O<sub>5</sub> response genotypes from two seasons in different locations and years.

Trials	Yield				
	82-83	83-84	83-85	84-85	85-86
Gainesville, FL 1964-1965 (n=194)					
25-87 1a					
82-83-1-8	0.20	-0.18	-0.11	0.24	0.84
83-87 1a					
83-84-1	0.05	-0.21	-0.20	-0.18	0.26
Yield 1a					
82-83-1-8	-	0.18	0.27*	0.26	0.21
Gainesville, FL 1965-1966 (n=18)					
85-86 1a					
82-83-2-8	0.48*	0.50	0.58	-0.15	0.17
85-87 1a					
83-84-1	0.11	0.28	-0.13	0.18	0.68
Yield 1a					
82-83-2-8	-	0.18	0.28	0.15	0.14

\*Significant, Florida, Gainesville, Martin County, Florida, - significance at 5%, 5%.



1996 to be linked with at least another yield-determining trait. In order to be a useful selection criterion in breeding for higher yielding systems,

### Conclusions

Simulation studies and field experiments, performed with random 87 ecotypes generated from one cross in two years, showed that weak positive associations can be present between yield and both 87F and 87S within environments. The linear regression model of yield as a function of either 87F or 87S explained small portions of the yield differences among genotypes within environments.

In all cases, similar weak positive relationships were observed between yield and 85-87 within environments. Correlations were positive and sometimes significant (0.03 to 0.31). However, the linear regression model of yield as a function of 85-87 explained only small portions of the yield differences among random genotypes within environments. Therefore, selection for long filling periods (87F, 87S, and 85-87) did not necessarily imply selection for higher yields within environments. These results are interpreted to suggest that seed growth rate as a late seed basis may be a more important yield-determining factor than filling period duration.

Simulations indicated, that weak positive associations between yield and physiological measures of seed filling duration (87F and 87S) can be expected, due to the

differential influence of DMAC, IRRAS, and PRAE, on yield and seed filling duration. The highest yield was observed in the simulated genotype with the longest IRR, highest IRRAS and PRAE, and lowest DMAC levels.

Consistent and low correlations between yield and duration of the filling period (IRR, IRRD, and IR-SD) were observed across environments. Therefore, it appears that the prospects of utilizing the length of seed filling as a selection criterion to select for higher yields among breeding lines are rather limited.

CHAPTER V  
ASSOCIATIONS BETWEEN YIELD AND SEED GROWTH RATE OF AN  
INDIVIDUAL SEED AND LARG AREA SEEDS

Introduction

Final seed yield of a crop results from the interaction of a large number of processes that take place throughout the growing cycle. Individual Seed Growth Rate (ISR) is a process that integrates many other processes and contributes to seed yield. However, Bell (1971) found that ISR estimated during the linear phase of seed growth was not an important yield-determining factor among four soybean cultivars. He found significant differences in ISR among cultivars, and a negative but nonsignificant correlation between yield and ISR. Number of seeds per unit area was an important trait correlated with yield within and across environments.

Bell (1971) found that once the linear phase of seed growth had started, ISR was not affected by short-term environmental stresses which resulted in reduced assimilate production. Defoliation and depodding experiments of Bell and Leggett (1971) showed that assimilate stored in vegetative tissues served as buffers to maintain near constant ISR for several weeks. These results suggest that the rate of soybean seed growth within environments was controlled to a large extent by mechanisms within the seed.

Environmental factors may also influence IGR. Egli (1975) reported considerable variation among some cultivars in IGR across planting dates. Lower IGR were observed by Egli et al. (1978) in various soybean cultivars in a year when lower temperatures were present. Lower temperatures also reduced peanut fruit growth rates under controlled conditions (Greer et al., 1981). Thus differences in IGR across environments should be expected. Further studies should provide information on the existence of genotype by environment interactions for IGR.

Soybean genotypes with larger seeds exhibited higher IGR, but IGR's were relatively constant across early and late formed pods (Egli et al., 1978). In other cultivars, however, late maturing seeds consistently had faster IGR (Ming and Greenwood, 1984a). The timing of IGR initiation was sequential in pods from different strains within plants in an indeterminate genotype (Spain and Sinclair, 1984a). Therefore, IGR should be determined on a whole plant basis, if meaningful comparisons between genotypes are to be made.

Seed growth rate on a land area basis (IGR) as calculated with IGR, is the product of IGR times the number of seeds that are actually growing per unit area. Therefore, seed yield results directly from IGR and the length of time this process is sustained by the plant. The relationship between IGR, the process that ultimately leads to seed yield, and yield itself appears to be inconsistent

in soybeans, high soybean genotypes differing in seed yield exhibited similar OSR (Kilgus and Weber, 1971a). Significant differences in OSR were observed in four soybean cultivars which did not exhibit yield differences (Kilgus and Seiler, 1971a), differences in OSR between two genotypes were detected in one year when yields were similar (Byli and Leggett 1971). In all these cases OSR differences were not related to yield differences.

Bedford (1979) observed a significant (P < 0.01) positive correlation between seed yield and OSR among eight soybean genotypes. In contrast, Byli and Leggett (1971) observed higher yields in two genotypes in a year when OSR's were lower. The existence of genotype by environment interaction for OSR was also suggested by the latter.

Genotypes in the studies cited above usually were unrelated, highly selected and high yielding selected varieties. In order to adequately represent trends within production standards etc. the associations of yield with both OSR and OSR should be determined among random genotypes within regions.

Estimates of OSR may lack precision. Carter et al. (1981) reported relatively high OSR's for dry weight analysis on different soybean crop growth analyses. Therefore a more precise means of estimating OSR would be desirable, to detect differences among genotypes using reasonable numbers of replications. In this work, OSR was calculated as the product of OSR from the number of mature seeds per plot,

While IGR estimated in this way was not mechanistically independent from yield, because seed number is a yield component, it was the only practical method available at the time, to precisely measure IGR.

The results presented in Chapter IV showed that a small portion of the yield differences among selected and random soybean genotypes from the crosses could be attributed to differences in the length of the filling period (measured as RFT, RPD, and RY-RFT). Such results indirectly suggested the possibility that IGR was a more important yield-determining factor than the length of seed filling.

Investigation on additional plant characteristics and processes that influence the association of yield with IGR would be helpful in understanding the complex interaction of factors from which seed yield results.

The objectives of this work were to examine the association between seed yield and IGR in simulated soybean genotypes, to determine the strength of the association of yield with both IGR and IGR among genotypes from the crosses under field conditions, and to compare the magnitude of genotype by environment interactions for IGR and IGR with that for yield among genotypes from crosses. Additional objectives were to examine, mainly with the use of the simulation model described in Chapter IV, the interaction of factors that influence the association of yield with IGR.

### Materials and Methods

A total of 48 simulated soybean genotypes were generated through sensitivity analyses of the phenomological model of soybean reproductive growth described in Chapter II. The initial inputs of the model tested in the sensitivity analyses were presented in Chapter IV. Yield and RGR values of the simulated genotypes were fitted to a linear regression model to formulate a hypothesis about the nature and strength of the association between these two traits.

The resulting hypothesis was then field tested using partial data from tests H2-D-1-D, H2-D-2-F, and H2-C-2. The materials and methods for these tests are described in Chapters II, III, and IV.

The materials used in 1982 were eight determinate RT soybean genotypes from each of the following crosses: Beasoba x Rutan (test H2-D-1-D) and Beasoba x R28-818 (test H2-D-2-F) described in Chapter II. Maxton, a released variety, was used as an additional check in the latter test. In 1983, a total of 18 genotypes from both crosses was studied in test H2-C-2.

Mean RGR was estimated as described in Chapter III. Seed growth rate on a land area basis (GRB) was calculated as the product of RGR times the number of mature seeds per plot, and expressed in kg/ha x day. Final Harvest Seed Weight (HSP) was determined using 250 mature seeds from each plot.

### Results and Discussion

#### Individual and Land Area Basis Total Growth Rates and Yield Differences Within and Across Replications

In all cases, the CV's for DCR were higher than the CV's for either ICR or seed yield (Tables 5.1 and 5.2). Nevertheless, the CV's for ICR and DCR were considerably lower than the ones reported by Carter et al. (1981) for several dry weight traits. Thus, in most cases, the methods used to estimate both ICR and DCR allowed the detection of significant differences among genotypes using only two and three replications in 1982 and 1983, respectively.

In 1982, significant differences for ICR were observed among genotypes within crosses (Table 5.1). In 1983, highly significant differences for ICR were detected among genotypes assembled from both crosses (Table 5.2). In 1982 differences in DCR were significant only among the genotypes from *Quince x Moringa* (Table 5.1). In 1983, significant differences for DCR were observed when genotypes from both crosses were combined (Table 5.2).

In 1982, yield differences were significant in Tests H1-G148 and H2-G148-F at the 50.0% and 8.15 levels, respectively, among the genotypes that were sequentially sampled (Table 5.3). In 1983, yield differences were highly significant among genotypes assembled from both crosses (Table 5.2).



Table 3-1. Individual Seed Growth Rate (1960), Seed Growth Rate on a Land Area Basis (1961), and Seed Yield of selected P2 soybean genotypes from our crosses in 1961.

Genotypes	1960	1961	1962
	mg/seed x day	kg/ha x day	kg/ha
	—————	Test 12-0-1-0	—————
Beaclone	4.14 bc	41.2 ab	1300 abc
Beaclone	4.14 bc	17.2 ab	1340 abc
P20-1310	4.14 bc	42.7 ab	1812 ab
P20-1314	4.15 a	44.8 ab	2738 bc
P20-1412	4.46 ab	48.2 ab	1588 c
P20-1418	4.11 bc	37.5 bc	1985 d
P20-1418	3.88 a	75.2 a	2437 a
P20-1434	3.75 c	40.8 a	1488 c
Mean	4.46	51.4	2151
CV	8.854	8.130	9.134
Signif.	P18.85	P10.04	P10.00
		————— Test 12-0-1-0 —————	
Beaclone	4.20 bc	45.4 a	1330 a
Beaclone	4.04 bc	72.8 a	1450 b
P20-018	3.45 c	73.5 a	1084 ab
P20-1454	4.12 bc	79.1 a	1818 ab
P20-1487	4.42 ab	88.1 a	1125 b
P20-1470	4.07 bc	78.5 a	2081 ab
P20-1481	4.01 ab	44.8 a	1148 b
P20-1320	4.04 bc	85.1 a	2071 b
P20-1316	4.08 b	81.6 a	2484 ab
Mean	4.22	74.2	2021
CV	8.858	6.147	9.138
Signif.	P18.87	ns	P10.10

(1) Means followed by the same letters are not significantly different at P18-85 level.

Table 3.6: Individual Seed Growth Rate (ISGR), Seed Growth Rate on a land area basis (SGR), and seed yield of selected P<sup>1</sup> soybean phenotypes from the crosses *Hamaker x Boyton* and *Hamaker x P10-478* in Year 1 (2002).

Genotypes	ISGR		SGR		Yield	
	mg/seed x day		kg/ha x day		kg/ha	
BOYTON	5.10	adill	81.4	bad	1115	c-d
Hamaker	5.85	a-d	81.0	abc	1010	a
P10-478	4.87	b-c	80.7	abc	1010	abc
PT9-1101	4.80	abc	80.3	ab	1008	a
PT9-1103	4.87	bcg	80.3	a-d	2794	ab
PT9-1194	5.33	ab	79.4	a-d	2807	a-d
PT9-1401	4.63	b-c	83.5	a-d	3040	a-b
PT9-1410	4.23	cde	74.8	a-d	2850	ab
PT9-1414	5.43	a	88.7	a	2760	ab
PT9-1423	5.40	ab	79.4	a-d	2829	abc
PT9-1426	4.93	a-d	84.0	a	2080	cde
PT9-1430	4.53	b-c	81.3	a	1857	c
PT9-1481	4.83	a-c	81.5	bad	2181	c-d
PT9-1485	4.98	a-d	83.8	a-d	2363	cde
PT9-1477	4.53	cde	71.3	a-d	2195	b-c
PT9-1487	4.87	b-c	88.8	a-d	2300	cde
PT9-1493	5.43	a-d	88.0	a-d	2315	cde
PT9-1505	3.80	e	82.3	a	2807	ac
PT9-1508	4.80	b-c	89.1	abc	1543	a-d
PT9-1509	5.87	ab	87.8	ab	2610	c-d
Mean	4.85		80.3		1398	
CV	0.118		4.175		0.113	
Signif.	P=0.81		P=0.02		P=0.81	

(1) Means followed by the same letter are not significantly different at 0.05 level.

Differences across environments were significant for 1968 only among genotypes in Test 42-0-1-B (Table 5-3). The genotype by environment interaction effects were nonsignificant for 1968 and 50B, but nearly significant ( $P=0.01$ ) for yield, among the same set of genotypes in Test 42-0-1-B. Thus 1968 and 50B exhibited more stability than yield across environments.

#### Associations Between Individual Seed Growth Rate and Other Traits

Genotypes that exhibited higher 196B tended to have higher values for seed weight (Table 5-4). However, the magnitude of the positive correlation between 196B and 50B was different among experiments.

The positive correlation between 196B and 50B was significant in two of three experiments (Table 5-4), but only a small portion of the variation in 50B could be attributed to 196B as shown by the relatively low correlation coefficients. These results are interpreted to suggest that genotypes which grow more seeds per unit area tended to produce higher 50B, or vice versa.

Associations between 196B on a whole plant basis and seed yield were similar to that reported by Agil (1975). In two of three experiments, low positive correlations were present between 196B and seed yield (Table 5-4). In Test 42-0-1 these two traits were not associated. Therefore, 196B appears to be a poor yield-determining factor among

Table 3.1. Mean squares from the analysis of variance for individual Seed Growth Rate (SGR), Seed Growth Rate on a seed area basis (SGR<sub>a</sub>), and seed yield among selected F<sub>2</sub> genotypes across Texas F1-C-0-0 and F1-C-0-3

Source of Variation	df	SGR	SGR <sub>a</sub>	Yield
Environments	1	157.2	1264.2	796529
Blocks(Env.)	3	55.8	44.3	189789
Genotypes	9	51.4121	349.9	447393
Gen. × Env.	9	12.7	97.7	321866-11)
Total	14	11.8	113.0	86615

11). 12) Significant at P=0.05 and P=0.02 levels, respectively

TABLE 2.4. Phenotypic correlation coefficients (r) between (individual) seed growth rate (SDGR) and either STRLS, and between mature hundred seed weight (SHWT) and seed yield in three experiments.

Trait	Year		
	87-88-89	88-89-90	89-90-91
SDGR vs. SHWT	0.48	0.71*	0.79**
SDGR vs. STR	0.79*	0.30	0.47*
SDGR vs. yield	0.39	0.84	0.30
SHWT vs. Yield	0.34*	0.63	0.58**

\*,\*\* Significant at P=0.05 and P=0.01 levels, respectively.

genotypes from these crosses;

Correlations between seed yield and ICR were positive but not significant in all experiments (Tables 3.3), consequently it appears that yield was more closely associated with seed number per unit of land area.

#### Association between Seed Yield and Seed Density per Unit of Land Area Area

Contrary to some previous results (Hewsey and Weber, 1974a; Kaplan and Bolter, 1974) and Sola and Leggett, 1976, a positive and highly significant association between yield and ICR was observed among simulated genotypes (Fig. 3.1b). The linear regression of yield as a function of ICR explained 81% of the yield variations.

In all cases, field results confirmed the prediction of the simulations. On each experiment, most of the yield differences were explained by the linear regression of yield as a function of ICR (Fig. 3.2, 3.3, and 3.4). However, seed yield is a function of seed number times seed size and ICR is a function of ICR times seed number. Since seed number is a component of both yield and ICR, these two values are not statistically independent. Thus, calculated  $R^2$  values overestimate real  $R^2$  values were undetermined amount. The relationship between yield and ICR was apparent even among the genotypes in Test E1-2-2-F (Fig. 3.1), where ICR values ranged from almost 0 to 20 kg/ha/day but were not significantly different among genotypes (Table 3.1). In

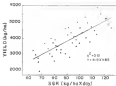


Figure 2 1: Association between seed yield and Seed Growth Rate on a land area basis (2000) among simulated soybean genotypes.

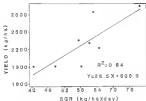


Figure 5.2. Relationship between seed yield and Seed Growth Rate in a land area based (LDB) using soybean genotypes in Dist. 12-2-3-6.



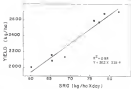


Figure 5/3. Relationship between seed yield and seed growth rate of a land area made (GRG) (kg/ha) soybean genotypes in Test 80-0-1-0.

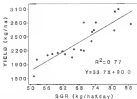


Figure 5.4. Association between seed yield and Seed Growth Rate in a land area (area) (SGR) under soybean genotype is Test 83-0-3.

these studies, the relationship between yield and GCR was determined among genotypes chosen to represent yield differences. Both simulations and field results as well as the lack of a strong association between yield and different estimates of the filling period among random genotypes (Chapter IV) support the idea that seed yield was mainly a function of GCR.

#### Factors Influencing the Association Between Yield and Seed Growth Rate

Most of the yield variance among simulated and field grown soybean genotypes was explained by differences in GCR. The plot of yield as a function of GCR, in which the observations on each of 18 simulated genotypes are shown (Fig. 3.3), provides the opportunity to examine which factors were mainly responsible for this close association as previously shown in Fig. 3.1. The  $R^2$  value for the linear model was 0.75. The highest seed yield was observed in the simulated genotype which simultaneously presented a combination of the highest DRMR and PRMR, with the lowest DRAC, and one of the highest GCR (Fig. 3.3). Conversely, the lowest seed yield was observed in the simulated genotype with the lowest DRMR and PRMR, the highest DRAC, and almost the lowest GCR.

Within a given PRMR and DRMR level, yield and GCR increased linearly as a function of DRMR in simulated genotypes (Fig. 3.3). Field results from Sept 13-15-2

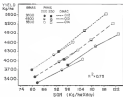


Figure 3-5 Factors influencing the relationship between seed yield and seed growth rate on a land area basis (GSR) among isolated soybean genotypes.

supported this hypothesis. Correlations were  $r=0.34^{**}$  ( $n=32$ ) between seed yield and LRAI, and  $r=0.55^{**}$  ( $n=32$ ) between SDR and LRAI. The LAI values at the beginning of seed growth in the simulations were approximately 2.4, 3.4, and 4.1, respectively, when LRAI values were 1100, 1500, and 1900 kg/ha. Madsen and Weber (1995) observed a linear increase in dry matter production with increases in solar radiation interception at similar LAI values. Therefore, the yield increases in the simulations due to increases in LRAI should be attributed to greater solar radiation interception, and to additional assimilation that may be mobilized to seeds.

In the simulations increases in FRAT resulted in yield and SDR increases only when the LRAI levels were maintained or increased and LRAI levels were maintained or decreased (Fig. 3.10). An example of the possible interactions among these factors are the few genotypes that reached yields of 1200 to 1600 kg/ha through different combinations of these three factors. Thus, similar yield levels can be reached through different avenues. The lack of yield increases with FRAT increases when other factors changed, supports a possible explanation for the relatively large portions of the yield variation that remained unexplained by the variation in canopy photosynthesis across several soybean genotypes reported by Wells et al. (1993).

Simulations suggest that selection for higher FRAT among genotypes of similar LRAI and SDR levels would

result in higher yield levels (Fig. 5.5). Since  $PMR$  is the rate of potential maximum dry biomass production of the crop resulting from photosynthesis, the selection proposed above would result from higher photosynthetic rates on a land area basis.

Decreases in  $DMAC$  at a given  $IPMR$  and  $PMR$  level among simulated genotypes produced a smaller small decrease in  $SEB$  but a strong increase in yield due to increases in the duration of seed filling (Fig. 5.5). The strong negative association between  $DMAC$  and different estimates of the duration of seed filling ( $SPF$ ,  $RFO$ , and  $R1-R7$ ) observed in field-grown soybean genotypes (Chapter VII) supports this hypothesis. These results suggest that lower  $DMAC$  values may be found in experiments where lower  $SPF$ , longer seed filling periods, and higher yields are observed.

Five simulated genotypes exhibited essentially similar  $SEB$  (42 to 48 kg/ha x day) while their yields differed by almost 20% (Fig. 5.5). It appears that the yield differences between these genotypes were mainly due to  $DMAC$  differences. Thus,  $DMAC$  differences may be one of the factors related to the yield differences observed in experiments among genotypes of similar  $SEB$ . In this case  $DMAC$  differences would be related to differences in the length of seed filling.

### Conclusions

The results were obtained using as a whole plant basis, and not earlier previously. The CV's were about half the magnitude of those previously reported for dry weight traits. Significant differences for DM and GR were detected in most cases using only two or three replications. Differences in GR were nonsignificant in only one of three experiments.

Individual seed growth rate and GR showed greater stability than yield across environments. Genotypes by environment interaction effects were not significant for DM and GR but were nearly significant ( $P < .10$ ) for yield, among the genotypes studied.

Seed yield had weak positive associations with DM in genotypes from two crosses. Genotypes that exhibited higher DM tended to have greater average seed weight. In one of three experiments, about half of the yield variation was explained by DM, and consequently most of the yield variation in the other experiments could be attributed to variation in the number of seeds per unit area.

Contrary to some studies in which recurrent selections were used, simulations predicted a positive and highly significant association between seed yield and GR. In all cases, field results confirmed such predictions. Most of the yield differences were explained by the linear regression

of yield as a function of  $\phi_{GR}$ . The lack of a strong association between yield and EFP observed in Chapter IV among the same genotypes also supports the idea that seed yield was primarily a function of  $\phi_{GR}$ .

Increases in  $\phi_{GR}$  and  $\phi_{RAE}$  tended to increase yield and  $\phi_{GR}$ , while DRAC increases tended to decrease both yield and  $\phi_{GR}$  among simulated genotypes. Field results on  $\phi_{GR}$  and  $\phi_{RAE}$  support this hypothesis. Maximum yield levels can be reached through several pathways due to the interaction of these factors and the length of seed filling. Yet the highest yields were observed in the simulated genotype with longest seed filling period, lowest  $\phi_{RAE}$ , and almost the highest  $\phi_{GR}$ .



CHAPTER VI  
ASSOCIATIONS OF DRY MATTER ALLOCATION COEFFICIENT WITH  
YIELD, LENGTH OF SEED FILLING, AND OTHER TRAITS

INTRODUCTION

Dry Matter Allocation Coefficient (DMAC) is based on the rate of linear harvest index (HI) increase of soybeans during seed filling, when HI is calculated disregarding fallen leaves (Galea Navarro et al. 1994). Since HI is the ratio of seed dry weight to total plant dry weight, DMAC characterizes the rate at which dry matter is allocated or partitioned to seeds during seed filling.

A negative but nonsignificant association between yield and DMAC was observed among eight soybean genotypes of different maturity (Galea Navarro et al. 1994). The weak negative association between yield and DMAC is important, because it indicates that seeds may be growing, to a certain extent, at the expense of assimilates stored in vegetative organs. If this process is accentuated in soybean plants, DMAC may be a yield-limiting factor. The type and strength of the association between yield and DMAC should be determined further among random genotypes within species.

Salido-Servino et al. (1984) observed that the highest yielding genotypes tended to exhibit both low DMAC and high seed growth rates (GSR) on a land area basis. More information is needed on this subject to better understand the interrelationship of these two processes that ultimately lead to soybean yield.

Yield ultimately depends on DM and the duration of the seed filling period. It follows that factors limiting either DM or the duration of seed filling may also limit seed yield. Sinclair and de Wit (1975) postulated that the high nitrogen demand of soybean seeds due to their higher protein concentrations, relative to other crops, limits the length of the seed filling period and yield of soybeans. Information is needed on the association of seed protein percentage and the length of seed filling in soybeans that would indicate if N is the primary basis of the self-destructive mechanism.

Salido-Servino et al. (1984) observed a strong negative association between DMAC and the length of the filling period (R<sup>2</sup>=0.7) in eight genotypes of different origin. Thus it appears that high DMAC values are another factor that limits the length of seed and filling in soybeans.

The basis for the negative association between DMAC and seed filling duration has not been clearly determined. Salido-Servino et al. (1984) reported a positive association between DMAC and seed protein percentage in a limited

number of genotypes. Studies on this subject should be done among random genotypes within strains, to adequately represent trends within populations.

The following approach was used in this work:

a) Hypotheses about the associations of DMAC with yield, SDP, and filling period estimates were examined using the simulation model of soybean reproductive growth described in Chapter III. b) Resulting hypotheses were field tested using six real random F7 determinate genotypes from two crosses, in two years.

Objectives of this work were: 1) to determine the type and strength of the associations of DMAC with yield among random genotypes, 2) to determine the mean contribution of DMAC and SDP to yield among selected genotypes, and 3) to determine the relationships among DMAC, seed filling duration, and seed protein percentage in random genotypes. Additional objectives were to examine additional factors which influence the associations of DMAC with the length of seed filling, and to estimate the stability of DMAC across environments and its broad sense heritability.

### Materials and Methods

The 48 simulated soybean genotypes described in Chapter II were used to examine hypotheses about the relationships of DMAC with yield, SDP, and seed filling duration estimates (SDP and SDPD). Simulated data were fitted to linear regression models to formulate the

hypotheses that were subsequently tested in field experiments.

The materials and methods used in the field experiments are described in previous chapters. Partial data from four field experiments (Tests H-0-1-e, H-0-1-f, H-0-1-i, and H-0-1-j) are presented in this chapter. The first two experiments and the last one were crop growth analyses in which DMAC, GGR, PRO, and HTF were measured in addition to yield, seed protein percentage, and the length of the period H-0-1. Test H-0-1 was intended only to determine yield, seed protein percentage, and H-0-1.

### Results and Discussion

#### DMC Similarity Coefficients From Two Sampling Dates

In 1983, highly significant differences in DMAC (estimated from two sampling dates) and seed yield were observed among 44 genotypes from each cross (Tests H-0-1-e and H-0-1-f). Average DMAC and seed yield of the genotypes from each cross are presented in Table 4.1 along with other statistics for these two traits. In 1983, highly significant DMAC differences were observed in Test H-0-1, among a total of 18 genotypes from both crosses which excluded the respective parents (Table 4.2). Similar DMAC differences were also observed in 1981 within each cross. In the group of genotypes that were repeated in 1981 (Table 4.2), highly significant yield differences were observed in

Table 4: Mean, minimum and maximum value, and standard deviation of DMAC and seed yield of 44 random F7 genotypes from two crosses and their respective parents in 1997.

	<u>Parents x 200180</u>		<u>Parents x 200178</u>	
	DMAC	Yield	DMAC	Yield
	day <sup>-1</sup>	kg/ha	day <sup>-1</sup>	kg/ha
Mean	0.8133	2642	0.8036	2187
Max. value	0.8137	2718	0.8054	2494
Min. value	0.8127	1353	0.8016	1353
Stand. dev.	0.0011	323	0.0018	318

Table 6.2 Dry Matter Allocation Coefficients (DMAC) on enlarged P2 genotypes in Years 12-14-16, 12-13-17, and 12-14-17.

Genotypes	1982		1983	
	Test 12-13-17 <sup>a</sup>		Test 12-14-17 <sup>a</sup>	
Boonika	0.0134	abc (1)	0.0130	abc
Wabian	0.0127	bc	0.0113	d
P29-1391	0.0110	de	0.0100	de
P29-1393	0.0107	e	0.0117	d
P29-1394	0.0108	de	0.0120	cd
P29-1405	0.0083	abc	0.0117	abc
P29-1410	0.0050	a	0.0120	cd
P29-1418	0.0010	a-d	0.0120	abcd
P29-1420	0.0008	de	0.0107	d
P29-1428	0.0128	cd	0.0120	cd
P29-1430	0.0130	a	0.0140	abc
CV	0.021			
Test 12-13-17				
Boonika	0.0124	bc	0.0110	abc
Wabian	0.0124	a	0.0040	de
P29-1401	0.0100	a	0.0010	a-d
P29-1405	0.0100	ab	0.0008	a
P29-1407	0.0100	cd	0.0110	d
P29-1408	0.0040	de	0.0140	abc
P29-1409	0.0008	cd	0.0130	cd
P29-1500	0.0110	a	0.0100	cd
P29-1508	0.0110	a	0.0120	cd
P29-1509	0.0120	de	0.0120	cd
CV	0.008		0.004	

(1) Means not followed by the same letter are significantly different at P=0.05.

Test 11-0-1 among the 22 genotypes from both crosses which included the respective parents. Average yield was 2188 kg/ha, and the highest and lowest yields were 3188 kg/ha and 1437 kg/ha, respectively, for P79-1151 and P79-2421.

In 1982, CV's for DMAC were 8.88% and 9.67%, respectively, in Tests 12-0-1-B and 13-0-1-F. Calculations were based on 44 genotypes per cross, two replications per genotype, two sampling dates per replication, and three plants per sampling date. In 1983, estimates of DMAC based on the same procedure but from three replications per genotype had a CV=9.02%. Carter et al. (1986) reported the more than twice as large for a number of dry weight traits from mixed crop growth analysis. Therefore, considerably less sampling effort and handling of material would be required to estimate DMAC at a given precision level, compared with other dry weight traits.

#### Relationship Between Dry Matter Accumulation Coefficients and Seed Yield

A negative association between DMAC and seed yield among simulated soybean genotypes was predicted from data generated by the model (Table 4.1). Results of field experiments performed in two years on a number of genotypes from two crosses support this hypothesis. In all cases the correlations between DMAC and seed yield were negative (Table 4.2). The associations between DMAC and seed yield among simulated and field grown random and selected

Table 4.1 Phenotypic correlation coefficients (r) between Dry Matter Elimination Coefficient (DMEC) with both seed yield and ST-67 in simulated and field grown soybean genotypes from two crosses.

Traits	Simulated genotypes (n=50)	1992	1993	1994
		Mean	Mean	Mean
		$\bar{x}$ Mean (n=40)	$\bar{x}$ Mean (n=40)	$\bar{x}$ Combined (n=20)
DMEC vs. Yield	-0.44**	-0.38	-0.39	-0.49
DMEC vs. ST6	-0.83**	-0.84**	-0.79**	-0.85**
DMEC vs. ST-67	*	-0.33*	-0.21*	-0.40**

\*,\*\* Significant at P=0.05 and 0.01 levels, respectively.



phenotypes were similar to the results of *Phase II* (Table 4.1) (1964).

Seed Yield as a Function of Dry Matter Allocation  
Cooperation and Seed Growth Rate in a Low Soil Moisture

Seed yield results ultimately from the combination of two associated processes: partitioning of assimilates from vegetative to reproductive organs and seed dry weight accumulation per unit of land area. Since DMAC reflects the rate of partitioning of assimilates estimated as dry matter, the expression of yield as a function of DMAC and GRM may explain most of the yield variation in a population of genotypes. The results observed in simulated genotypes support this hypothesis. All the yield variation was explained by the regression on DMAC and GRM (Fig. 4.2). The resulting response surface was a plane which shows that simulated genotypes with the highest yields were the ones with high GRM and low DMAC values.

Data on field grown soybean genotypes from two crosses (Test 11-0-2) showed close agreement with the trend predicted by simulated genotypes for the regression of yield as a function of DMAC and GRM (Fig. 4.2). Similar results were obtained in Tests 11-0-3-6, in Test 11-0-3-7 the DMAC effect was non-significant.

It follows that when DMAC's were higher the daily supply of plant assimilates was not sufficient to maintain the GRM obtained. Consequently, more assimilates were

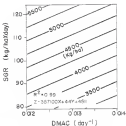


Figure 4.1 Seed yield as a function of the Dry Matter Allocation Coefficient (DMAC) and Seed Growth Rate on a land area basis (SGR) among simulated soybean genotypes

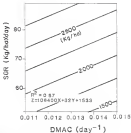


Figure 4-2: Seed yield as a function of the Day Seedling Elimination Coefficient (DMAC) and Seed Growth Rate on a Land Area Basis (SGRB), among determinate soybean genotypes in test 11-3-2.

transitioned from vegetative to reproductive growth to meet above ground demands, causing depletion of vegetative dry matter. Whether this effect in field grown soybeans is mainly due to the translocation of N, as proposed by Hunsaker and de Wit (1975, 1978), or to carbohydrates, or both, should be determined. Whatever the nature of the self-destruct mechanism, these results support the idea that this mechanism exists during seed filling in the soybean plant.

#### Association of Dry Matter Regression Coefficients With Relative Plant Height, Reproductive Period Duration, and R<sup>2</sup>

A strong negative association between RFP and GRAC was predicted by the simulated soybean genotypes (Fig. 5.3). These data were generated by simulating a combination of five GRAC's with three biomass at the beginning of seed growth (GRAC1), and three potential maximum biomass seed growth rates (GRAC2). Results from two field experiments, each with eight selected determinate RT soybean genotypes from the crosses Bonanza x Batten and Bonanza x 789-438 in one year, and 10 selected genotypes in another year, actually support the hypothesis formulated with the model. In 1980, the correlation coefficients between RFP and GRAC were  $r = -0.81$  ( $n=8$ ) and  $r = -0.88$  ( $n=10$ ), respectively for Batts RI-0-1-0 and RI-0-1-0. The positive correlation in Batts RI-0-1-0 may be an artifact caused by the small range in RFP (11 to 18 days). In 1981, a negative association

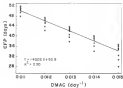


Figure 8.3: Minimum Filling Period (RFP) as a function of Dry Matter Allocation Coefficient (DMAC), using simulated soybean genotypes

between IPP and DMAC was observed in Test H-3-2 (Fig. 4.4).

By definition IPP is the ratio of final SD to DMAC, thus a close negative association between IPP and DMAC should be expected. Results from simulations and field data fully support this idea. Highly significant negative associations between IPP and DMAC were always present, and DMAC differences explained to a great extent IPP differences in each experiment (Table 3.1). Furthermore, regressions of IPP as a function of DMAC using data from the field experiments predicted a decline in IPP of 1.1 to 2.7 days for every  $1,001 \text{ kg}^{-1}$  increase in DMAC observed.

In both years, the visual estimate of the length of seed filling, SI-ST, also showed significant or highly significant negative associations with DMAC, among genotypes from two crosses (Table 4.1). These results further support the hypothesis that a strong negative association exists between DMAC and the duration of seed filling in soybeans. It follows that DMAC indicates the intensity of the seed destruction in the soybean plant, irrespective of the nature of the limiting substrate being partitioned to seeds.

The plot of IPP as a function of DMAC in which the characteristics of simulated genotypes are presented (Fig. 4.5), offers the opportunity to examine which additional characteristics influence the strong negative association observed in field experiments and in simulated genotypes

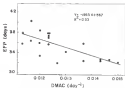


Figure 4.4 Effective Filling Period (EFP) as a function of Dry Matter Allocation Coefficient (DMAC), among selected FT genotypes in Test 10-0-2.

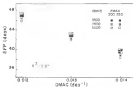


Figure 8.8. Factors influencing the association between Effective Filling Fraction (EFF) and Ray-Walker Alignment Coefficient (RWAC) among simulated soybean genotypes.



(Fig. 4.10) between these two traits. The length of EFP was primarily shortened by higher DMAC values, and only minor changes were observed in EFP with varying in RRP and PRAC levels in selected genotypes. These analogous results are in agreement with the results observed for the relationship between yield and EFP (Fig. 4.11) discussed in Chapter IV.

#### Relationships of Seed Protein Percentage with Dry Matter Allocation, DMAC, and Length of Root System

As stated before, the strong negative association between DMAC and different estimates of the length of root filling, and the weak negative association of DMAC with yield suggest the existence of a self-destructive mechanism in soybeans during seed filling. The availability of random genotypes with different seed protein percentages provided the opportunity to test whether higher seed N percentage is a limiting factor in the self-destructive mechanism as proposed by Sinclair and de Wit (1975, 1978).

Correlations of seed protein percentage with DMAC, EFP, and RS-EF were usually nonsignificant and inconsistent over experiments and crosses (Table 8.4). Correlations between seed protein percentage and DMAC were significant and negative in Test 81-0-1-2, while in Test 81-0-3 the average was zero. A nearly significant positive correlation was observed. A significant negative correlation between seed protein percentage and RS-EF was observed in Test 81-0-1. In general, correlations did not show a consistent

Table S.4. Phenotypic correlation coefficients between seed protein percentage, Dry Matter Allocation Coefficient (DMAC), Reproductive period duration (RPD), and  $\alpha$ -D<sup>+</sup>.

Test	Seed Protein vs DMAC	Seed Protein vs RPD	Seed Protein vs RPD- $\alpha$
Soybean (Soybean) 2			
$\alpha$ -D <sup>+</sup> - $\alpha$	-0.29* (n=12)	-0.16 (n=12)	0.23 (n=12)
$\alpha$ -D <sup>+</sup> - $\alpha$	-0.04 (n=12)	-0.17 (n=12)	0.30 (n=12)
$\alpha$ -D <sup>+</sup> - $\alpha$	-	-	-0.37* (n=12)
$\alpha$ -D <sup>+</sup> - $\alpha$	0.40 (1) (n=12)	-0.12 (n=12)	0.06 (n=12)

\* Denotes significance at  $P \leq 0.05$ .

|| Denotes significance at  $P \leq 0.01$ .

positive or negative association of soybean seed volume percentage with DMAC or the length of the seed falling period. The results do not provide enough evidence to support or reject the idea that it is the basis of the self-destructive mechanism that shortens the length of the soybean falling period as proposed by Hoadley and de Wit (1979,1976). Therefore, the nature of the self-destructive mechanism remains undetermined. Perhaps both B and C as an energy equivalent basis, are responsible for the self-destruction of the soybean plant that appears to take place due to seed density that exceed the daily supply of plant assimilates.

#### Stability Across Environments, and Seed Mass Reliability of Soy Soybean Allotment Contrasting

The analysis of DMAC across 1982 and 1983 for the genotypes from Hancock & Sutton showed no significant year effects but nearly significant IPB,SD differences among genotypes (Table 4.1), while yield exhibited a significant genotype by environment interaction effect.

The DMAC of genotypes from Hancock & Sutton also showed a different behavior across environments, compared to yield. In this case the genotype by environment interaction effect was significant for DMAC and non-significant for yield (Table 4.2).

Seed mass heritability estimates for DMAC were similar or lower than for yield among the genotypes from

Table 5.5 Data reported from the analysis of variance combined across 1982 and 1983 for dry matter allocation conditions (moist) and seed yield of selected P7 genotypes from two streams.

	Seedling at 10/10/82		Seedling at 10/10/83	
	Mean	SE	Mean	SE
Development	0.000000	0.000000	0.000000	0.000000
Allocation	0.000000	0.000000	0.000000	0.000000
Genotype	0.000000	0.000000	0.000000	0.000000
Gen x Dev.	0.000000	0.000000	0.000000	0.000000
Error	0.000000	0.000000	0.000000	0.000000
CV	0.000	0.000	0.000	0.000

a) Significant at 10/10/82 and 10/10/83, respectively.

b) Significant at 10/10/82.

with DMAC. Seed mass heritabilities were 0.4 and 0.08, respectively for DMAC and yield among 11 genotypes from *Maize* x *Perlon*, and 0.0 and 0.79, respectively, for DMAC and yield among 18 genotypes from *Maize* x *Perlon*. Therefore, selection for low DMAC would require replicated testing in different environments as was already suggested by a significant genotype by environment interaction found among the genotypes from *Maize* x *Perlon*.

### CONCLUSIONS

Seed yield and DMAC showed weak negative associations ( $r = -0.18$  to  $-0.05$ ) as predicted by the simulations ( $r = -0.40^{**}$ ). The regression of yield as a function of DMAC and HZ explained most of the yield variation among simulated and field-grown soybean genotypes. The highest yields can be observed in the region of lowest DMAC and highest HZ.

A negative association between HZ and DMAC was predicted by simulated genotypes and observed in two out of three field experiments. Linear increases in HZ were primarily due to lower DMAC as predicted by the model ( $\Delta Z = 0.52$ ), and confirmed in field experiments ( $\Delta Z = 0.43$  to  $0.70$ ). Furthermore, a significant and highly significant negative association between DMAC and HZ x HZ was found in field experiments ( $r = -0.36^{**}$  to  $-0.80^{**}$ ). The strong negative associations of DMAC with seed filling duration, and the weak negative association with yield, suggest the

existence of a self-destructive mechanism in soybeans during the filling period. Genotypes that tend to allocate or partition their dry matter more rapidly to seeds, do so at the expense of a greater decline in vegetative dry matter, and shorter seed filling period.

The basis of this self-destructive mechanism remains undetermined, because locomotion and non-significant correlations of seed protein percentage with DMAC and seed filling duration estimates did not support the idea that seed N percentage is the primary limiting factor. It appears then, that both C and N on an energy equivalent basis may be the limiting substrates pertained to seeds.

A significant genotype by environment interaction for DMAC was detected among the genotypes from one of the two crosses tested. Seed mass harvestability estimates for DMAC among the genotypes from two crosses (44.8 and 57.1 %) were somewhat lower than for yield (49.1 and 51.7 %). Therefore, selection for low DMAC would require replicated testing in different environments.

## CHAPTER VII SUMMARY AND CONCLUSIONS

### Associations between Yield and Seed Protein Percentage Within and between Environments

The overall objectives of this dissertation were a) to determine if the association between yield and seed protein percentage tends to be positive, when the high protein parent is the cross as well as the higher yielding parent; b) to compare a visual estimate of seed filling (dfl-off) with two physiological estimates of the length of seed filling (HFF and HFC), and c) to determine the associations among yield and physiological traits such as the length of seed filling, individual seed growth rate (ICGR), seed growth rate on a land area basis (LCGR), and the rate of dry matter allocation to seeds (DMAC) among other factors.

Based on data presented, the following conclusions appear to be justified, however, they may be restricted to cereals/cereals systems.

Seed negative associations can be expected in systems between yield and seed protein percentage if either higher or lower yielding parents are used as the high protein parent. Correlations between seed protein percentage and seed yield in several environments among parents and selected genotypes, from crosses where high protein parents were also the higher yielding parents, were similar to zero.

and magnitude to the ones reported when high yielding parents were the lower yielding parents.

Studies on yield and seed protein percentage should be performed across several environments to obtain average results. The sign and magnitude of the correlations between yield and seed protein percentage showed considerable variation across six environments, within crosses. Correlations ranged from  $r=0.11$  to  $-0.51^{**}$  in one cross, and from  $r=0.18$  to  $-0.43^{**}$  in another cross.

Associations between yield and seed protein percentage across low and medium-yielding environments did not show a tendency to become consistently negative and stronger in lower yielding environments. However, the lack of high-yielding environments prevented adequate testing of the hypothesis that seed protein percentage tends to increase in low-yielding, drought-stressed environments.

The amount of protein produced per unit of land area can be increased by seed yield increases, while the production of oil per unit area can be increased by either seed yield or seed oil percentage increases. In most cases, yield of protein and oil were a function of seed yield, and usually yields of protein were not associated with seed protein percentages. In six of 18 cases, positive correlations between yield of oil and seed oil percentage were significant or highly significant, but the  $r$  values were always considerably lower than those between yield of oil and seed yield.



5. New Physiological Variants of Seed Filling  
Estimates Based on Two Sampling Dates and Harvest Index

Linear  $RI$  increases during most of seed filling is a consistent feature of deterministic systems. Harvest index estimated disregarding fallen leaves increased linearly with time ( $R^2=0.91$ ) during seed filling in 17 genotypes. Self Remuda, one of the parents, showed a slightly lower fit to the linear model ( $R^2=0.83$ ).

Satisfactory estimates of DMAC, the rate of linear  $RI$  increase, were obtained using data from a few plants sampled twice (early and late) during seed filling. Estimates of DMAC based on two sampling dates can be used interchangeably with estimates of DMAC obtained from sequential samplings performed throughout seed filling. The CV's of DMAC estimates based on two sampling dates ranged between 0.074 and 0.094 among genotypes from two crosses in two years.

The linear  $RI$  increase during most of seed filling and the previous estimates of DMAC that can be obtained from two sampling dates provide the opportunity to characterize seed filling duration in a precise, physiologically sound, and relatively easy-to-obtain way.

Reproductive Period Duration (RPD), was defined as the time of final  $RI$  or DMAC (both estimated disregarding fallen leaves).

Comparisons between  
Physiological and Visual Estimates of Seed  
Filling Duration, and their Predictive Ability for Seed Weight

Estimates of mean ISEB on a whole plant basis obtained from only one early and one late sampling date can be used satisfactorily with estimates of ISEB obtained from sequential samplings performed throughout seed filling. Data on ISEB obtained from two samplings plus mature individual seed weight can be used to calculate EFP with relatively low CV's.

In all cases, mean ELSD and ELRI occurred simultaneously on numerous determinate genotypes from two crosses. Plants reached R5 10 to 18 days before either ELSD or ELRI, but observations among these three stages were positive and strong (POS.XI). Although R5 was an inaccurate indicator of ELSD and ELRI on determinate genotypes, it was an acceptably precise relative measure.

Mean ELSD on a whole plant basis was reached three to six days after mean ELSD in each genotype-determinant combination, and plants lost vegetative dry weight after ELSD was reached. In two of three cases, differences between ELRI and ELSD were significant. Stage R5 was an accurate and precise indicator of ELSD in two of three experiments on determinate plants.

Differences for EFP, RI-RT, and EFP can be found among any two genotypes. In all cases, highly significant differences for EFP and RI-RT were observed within experiments, while highly significant differences for EFP

were detected only in one of three experiments.

The association between EFP and RPO was positive but not consistently significant, because both periods started simultaneously but RPO continued for three to seven days longer.

The visual estimate of the length of seed filling, R5-R7, was not a consistent, precise, and accurate estimate of either EFP or RPO, because the period R5-R7 was 8 to 11 days longer than EFP, and slightly longer than RPO, using a number of determinate genotypes from two crosses.

The use of EFP, RPO or R5-R7 as selection criteria in system breeding appears to be limited in some extent, due to the significance of highly significant genotype by environment interactions and low heritability heritabilities that can be observed for these traits.

#### Development of a Simulation Model of Soybean Reproductive Growth

A simple simulation model of soybean reproductive growth was developed. The model is based on the assumption that events prior to seed growth limit seed yield only to the extent that vegetative dry weight restricts the flowering and development of seed. The primary purpose of the model was to examine hypotheses that have implications in system breeding rather than trying to mimic soybean growth.

The model incorporates the concept of DMAC into the context of soybean reproductive growth. Inputs to the model are: BMAD, PMAD, and DMAC. Different seed proteins and oil percentages as well as vegetative N percentages can also be simulated. Outputs of the model on a daily basis are leaf, vegetative, and seed dry weights, LAI, ST, DM, and seed N accumulation rates. The model terminates the simulations when LAI becomes negligible and plants are assumed to be mature. At crop maturity the model outputs include yield, final ST, and SPD. Extensive filling period can be calculated as the ratio of final seed weight to SDI during the linear portion of simulated seed growth.

#### Associations of Yield With Both Physiological and Yield Parameters of SPD, Filling Period

Simulation studies and field experiments with PT soybean genotypes show that weak positive associations can be observed between yield and both SPD and SPD within environments. The linear regression model of yield as a function of either SPD, SPD, or ST-SPD explained small portions of the yield differences among genotypes within environments.

Selection for long filling periods (SPD, SPD, and ST-SPD) does not consistently result in selection for higher yields within environments, because some genotypes with long seed filling periods had low yields. Conversely, though, genotypes with short seed filling periods rarely

had high yields. The  $R^2$  values can be somewhat higher in experiments where genotypes selected to represent differences in yield and seed filling period estimates are used. In these cases, variations in RGR explained about 60% of the yield variation. These results indirectly suggest that seed growth rate on a land area basis may be a more important yield-determining factor than seed filling duration in random soybean genotypes.

The weak positive associations observed between yield and different estimates of the length of seed filling can be explained by the differential influence that RGR had on yield and EFP among simulated genotypes. Within a given RGR level, increases in IGRS and FGRS produced sharp yield increases, but EFP remained essentially constant, while GRC increases (at constant IGRS and FGRS levels) produced a moderate reduction in yield and a large reduction in EFP.

#### Associations Between Yield and Seed Growth Rate on a Land Area Basis and Seed Filling Period

Individual seed growth rate on a whole plant basis and SGR can be measured rather precisely using a new method, although SGR estimates in this case are not chronologically independent of yield. The  $C_r$ 's for SGR can be about half the magnitude of those previously reported for dry weight basis in other soybean crop growth analyses. Thus, significant differences for IGRS and SGR can be detected

using two or three replications. Differences in SDH were nonsignificant in only one of three experiments.

Individual seed growth rate and SDH showed greater stability than yield across environments. Genotypes by environment interaction effects were not significant for 1968 and 1969 but were nearly significant ( $P=0.05$ ) for yield in one case, among the genotypes studied.

Weak positive associations between yield and SDH can be observed. Genotypes that exhibited higher SDH tended to have higher mature individual seed weight. In one of three experiments, about half of the yield variation was explained by mature seed weight. Similarly, only in one of three experiments about half of the variation in SDH could be attributed to SDH. Consequently, most of the variation in yield and SDH in the other experiments could be attributed to final seed number per unit of land area.

Contrary to some reports in which released varieties were studied, a positive and highly significant association between seed yield and SDH was observed among simulated genotypes. In all cases, final results among genotypes from two crosses confirmed such prediction. Most of the yield variation was explained by the linear regression of yield as a function of SDH.

The strong positive association between yield and SDH can be properly explained by the relationships that IRAD and PRAD had, with yield and SDH of simulated genotypes. Yield and SDH increased with increases in IRAD and PRAD

level). Smaller changes in yield and DM were observed with changes in DMAC. When DMAC increased, DM increased and yield decreased. The decrease in yield observed can be attributed to shorter seed filling periods.

When DMAC or DMAS increased, sharp yield increases were observed only if all other factors remained constant among simulated genotypes.

#### Identification of Key Factors Affecting Correlations with Yield, Filling Period, DMAC, and DMAS Values

Seed yield and DMAC showed weak negative associations ( $r=-0.14$  to  $-0.40$ ) in field experiments that were predicted by the model ( $r=-0.14$  to  $-0.19$ ). The regression of yield as a function of DMAC and DMAS explained most of the yield variation among simulated and field grown soybean genotypes. The resulting response surface was a plane in which the highest yields can be observed in the region of lowest DMAC and highest DMAS values.

A positive association between DMF and DMAC was predicted by the simulated genotypes and observed in two of three field experiments. Increases in DMF were primarily due to lower DMAC values as predicted by the simulation model ( $r^2=0.82$ ), and confirmed in field experiments ( $r^2=0.43$  to  $0.59$ ). Furthermore, a significant and highly significant negative association between DMAC and DM-07 was found in field experiments ( $r=-0.39$  to  $-0.48$ ). Small changes in DMF were observed with changes in DMAS and DMF

several simulated genotypes. Since DMAC indicates the rate of dry matter allocation or partitioned to seeds from vegetative organs, the above results indicate that shorter filling periods are positively associated with faster depletion of vegetative dry matter during seed filling. This supports the idea that a self-destructive mechanism of seed sink operates within the soybean plant.

The basis of the self-destructive mechanism remains unknown. Due to inconsistent and nonsignificant associations of seed protein percentage with DMAC and the length of seed filling observed in field grown soybeans. Perhaps the self-destructive mechanism is based on the energy equivalence of both the C and N compounds that are transferred from vegetative tissues to soybean seeds.

Selection for lower DMAC values requires replicated testing across environments, due to significant genotype by environment interactions and broad sense heritabilities similar or slightly lower than for yield.

#### Heritability Associated to Intrinsic Protein, Yield, and DMAC

Higher moderate yield levels can be obtained by simulated genotypes with different combinations of IRMS, RMS, and DMAC. Field data on IRMS and DMAC were in close agreement with this hypothesis. Therefore, moderate yield levels could be reached by several different pathways. However, the highest yield was observed only in the



selected genotypes with highest IRRAD, highest PHAR, and nearly the highest SGR that simultaneously exhibited the lowest CHAC and largest EFP.

Based on results from simulations and field experiments it appears that these theoretical approaches to increase yields are possible and can be pursued separately or in combination (Table 7.1). These approaches are a) to increase IRRAD, b) to increase PHAR, and c) to lower CHAC. Selection for yield could be simultaneous with selection for any one of the proposed traits, to ensure that the other traits do not decline and become limiting factors.

A fourth approach would be to select for higher SGR, since it was positive and highly associated with yield. As we show in Table 7.1 selection for either higher IRRAD or PHAR would increase SGR and consequently yield.

It is obvious that a crop requires a certain vegetative biomass level to intercept most of the solar radiation and support seed growth. Relative increases in IRRAD that would result in LAI values above the ones required for minimum light interception would tend to increase yield because of the greater availability of assimilate that potentially could be partitioned into seeds. Yield increases would be mainly due to SGR increases, and the length of seed filling should remain essentially unchanged. This strategy has been successfully applied to increase yield through increases in plant densities and narrow rows (Kropf 1979, 1971).

Table 1.1. Approaches to increase soybean seed yield through breeding.

Yield Attribute For	Breeding Effect on Seed Yield		
	SDR	STP	Days from planting to maturity
Greater DMGR	+	+	+
Greater PRAR	+	+	+
Lower DMAC	+	+	+

DMGR = DMGRASS, + Decrease, and + No change.

Increases in DMAC would be expected only in drought years, because lodging would tend to increase with larger plant size as reported by Harkness and Edwards (1970) and Cooper (1971), and probably to result in a decline.

Selection for higher DMAC would tend to increase yield in plants of similar DMAC and DMAC. This type of approach would increase yield mainly due to DM increases and thus would be especially applicable in regions where the length of seed filling and the growing cycle of the crop could not be suitably extended. Selection for yield would likely be the most efficient way to enhance DMAC if DMAC and DMAC are held constant.

Lowering DMAC levels would tend to minimize the rate of self destruction in detritivore exposed plants. Higher yields in this case would result primarily from considerable increases in the length of seed filling and slightly lower DM's.

Higher yielding genotypes would be the ones which intercept most of the incoming solar radiation and are able to sustain high concurrent DM's and crop growth rates for longer periods of time while maintaining low rates of vegetative dry matter depletion (low DMAC).

#### FEEDING APPROACHES TO IMPROVE SYSTEM YIELD THROUGH SEEDLING

Isabel Serrero (1981) hypothesized that simultaneous selection for higher final ht and longer seed filling

period, as soybean plants of similar average plant size under good growing conditions, would lead to higher yield. The results of this work are in close agreement with the above hypothesis.

Selection for higher RI has brought about smaller and earlier plants with lower yield (Hendall and Scherer, 1977). However, in plants of similar biomass, seed yield should be a function of final RI. The correlation coefficient of yield with final RI was  $r=0.92^{**}$  ( $n=15$ ) among simulated genotypes with LRRAD of 4000 kg/ha, three PHAS levels (150, 200, and 250 kg/handay), and five ORAC levels (4.813, 5.813, 6.813, 7.814, and 8.815  $\text{day}^{-1}$ ). Therefore, in plants of similar high biomass compatible with both structural effects as lodging, RI would be a suitable selection criterion. In this case, the stability of RI across plant sizes and environments observed by Specht et al. (1980) would be advantageous.

Interactions among simulated genotypes indicate that selection for high final RI among plants of similar biomass would imply indirect selection for higher PHAS, longer seed filling period, and higher GRN. The correlation coefficients of final RI were  $r=0.82^{**}$  with PHAS,  $0.71^{**}$  with RFP,  $0.65^{**}$  with RPP, and  $0.89^{**}$  with GRN among the 15 simulated genotypes with LRRAD of 4000 kg/ha that were mentioned above.

It was shown in Chapter IV that higher yields were consistently observed as ORAC decreased and PHAS increased.

among simulated genotypes of similar (4000 kg/ha) DMAD (Fig. 4.3.11). Therefore, to improve the chances of selecting the highest yielding genotypes, selection for lower DMAD should be carried out in addition to selection for higher final SI, in plants of similar biomass. The insignificant negative correlation between final SI and DMAD ( $r = -0.23$ ,  $n=11$ ), among simulated genotypes with final SI of 4000 kg/ha, indicates that selection for higher final SI does not necessarily imply selection for lower DMAD. However, the close negative association between estimates of the length of seed filling and DMAD, reported in Chapter VI, indicates that visual selection for longer seed filling period would be a practical way to select indirectly for lower DMAD.

Combining visual selection for long seed filling period and high SI in plants of similar biomass would counter the tendency toward earlier maturity among plants with higher SI, as was observed by Russell and Bunting (1977).

Visual selection of genotypes with high, approximately similar biomass at maturity, would probably be effective for practical purposes. The whole method of selection for high similar biomass, long filling period, and high SI would be possible using only short replicated rows, instead of plots as is usually necessary when testing for yield itself. Therefore, higher numbers of lines could be indirectly screened for yield in this way, as the step

will be useful for yield itself. In my view, to determine the advantages of this methodology over the conventional selection for yield, under practical breeding conditions, is one of the current primary challenges of systems research.

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TABLE 1	
Summary of the results of the analysis of variance for the effect of the treatment on the response of the different groups of subjects	
Treatment	Response
Control	1.00
1.00	1.00
2.00	1.00
3.00	1.00
4.00	1.00
5.00	1.00
6.00	1.00
7.00	1.00
8.00	1.00
9.00	1.00
10.00	1.00
11.00	1.00
12.00	1.00
13.00	1.00
14.00	1.00
15.00	1.00
16.00	1.00
17.00	1.00
18.00	1.00
19.00	1.00
20.00	1.00
21.00	1.00
22.00	1.00
23.00	1.00
24.00	1.00
25.00	1.00
26.00	1.00
27.00	1.00
28.00	1.00
29.00	1.00
30.00	1.00
31.00	1.00
32.00	1.00
33.00	1.00
34.00	1.00
35.00	1.00
36.00	1.00
37.00	1.00
38.00	1.00
39.00	1.00
40.00	1.00
41.00	1.00
42.00	1.00
43.00	1.00
44.00	1.00
45.00	1.00
46.00	1.00
47.00	1.00
48.00	1.00
49.00	1.00
50.00	1.00
51.00	1.00
52.00	1.00
53.00	1.00
54.00	1.00
55.00	1.00
56.00	1.00
57.00	1.00
58.00	1.00
59.00	1.00
60.00	1.00
61.00	1.00
62.00	1.00
63.00	1.00
64.00	1.00
65.00	1.00
66.00	1.00
67.00	1.00
68.00	1.00
69.00	1.00
70.00	1.00
71.00	1.00
72.00	1.00
73.00	1.00
74.00	1.00
75.00	1.00
76.00	1.00
77.00	1.00
78.00	1.00
79.00	1.00
80.00	1.00
81.00	1.00
82.00	1.00
83.00	1.00
84.00	1.00
85.00	1.00
86.00	1.00
87.00	1.00
88.00	1.00
89.00	1.00
90.00	1.00
91.00	1.00
92.00	1.00
93.00	1.00
94.00	1.00
95.00	1.00
96.00	1.00
97.00	1.00
98.00	1.00
99.00	1.00
100.00	1.00



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RESUME OF LIFE

Don José Saldaña Navarro was born 25 December 1948 in Catamarca, Argentina. He attended grammar school there at Colegio Pedro Juan de la Quintana and graduated from high school from Colegio Nacional Pío del Castillo in 1968. In 1968 he started a five year program of study at Universidad Nacional de Tucumán, in Argentina, where he graduated as Ingeniero Agrónomo in May 1971.

From 1971 until 1977 he worked in dry bean research and as Lecturer at the Agronomy Department of the Universidad Nacional de Tucumán. In September 1977 he joined the National Institute for Agricultural Technology (INTA) in Argentina, at the Regional Exp. Sta. of Tucumán, Tucumán. There he conducted field research on soybean management and variety trials, and started a soybean breeding program for North Western Argentina. In 1980, he enrolled in the University of Florida where he graduated with a Master of Science in Agronomy in 1982. From then on he pursued doctoral work in Agronomy at the University of Florida. He has been married since 1979 and has a dear son, Fernando.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

  
\_\_\_\_\_  
Earl E. Hines, Chairman  
Professor of Agronomy

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

  
\_\_\_\_\_  
Thomas R. Sinclair  
Adjunct Professor of  
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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

  
\_\_\_\_\_  
Earl E. Hines  
Professor of Agronomy

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December 1944

  
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